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THE FORMATION OF MECHANICAL TISSUE IN THE TENDRILS OF PASSIFLORA CAERULEA AS INFLUENCED BY TENSION AND CONTACT

W. D. BRUSH

(WITH THREE FIGURES)

Introduction

The mechanical theory of growth, as put forth by SACHS (**20**), has of late years been replaced by the idea of self-regulation in the plant depending upon external stimulus. This idea is followed quite closely by PFEFFER (**18**).[1] As a consequence, considerable attention has been directed to the effect of strain upon plant tissues, since by this new theory we might expect the plant to respond to a state of strain by a greater development of strengthening tissues. The present investigation was undertaken to determine if such self-regulation is present in the tendril that stronger mechanical tissues are produced where needed. To state the problem of the present paper: Do tendrils which are functioning to support the plant possess greater strength than those which have grasped no support, and if so, how is this strength increased, and is it due to tension or to contact, or to a combination of both?

DARWIN (**5**) observed that tendrils which have grasped no support soon die; WORGITZKY (**26**, p. 39) noted a greater breaking strength of tendrils with a support over those without. Otherwise, no attempt has been made to answer this question.

[1] For a discussion of these two theories see NEWCOMBE (**15**).

Historical

The first observations to determine the effect of strain upon the plant were by KNIGHT (12) in 1803, when he allowed fruit trees to sway in the wind in one plane only and obtained a greater increase in wood on the two sides in the direction of swaying; this he considered to be due to a greater movement of sap through a loosening of the cells, a merely mechanical process.

In 1879 BARANETSKY (2), investigating the periodicity of growth, found that when a small amount of tension (10–30 grams) was applied to a stem, it had the effect of retarding the growth in length.

SCHOLTZ (21) confirmed these observations, but found that two results were produced: first an acceleration and later a retardation of growth; the first result he attributes to a rapid growth of the cell-membrane, the second to a pathological condition in which the building up of the materials is hindered.

HEGLER (8), working along the same lines, found that this retardation of growth bears a close relation to the daily periodicity in elongation of the stem. This, he says, demonstrates that tension calls forth a response in the cell, hence is a true irritation stimulus.

HEGLER (9) also investigated the effect of tension upon the anatomical structure of stems. By gradually increasing tension on seedlings of various plants, he found that the breaking strength was in many cases nearly doubled in three days, due to an increase in amount of the collenchyma, sclerenchyma, and bast, a much greater increase than takes place under normal conditions.

BALL (1) later repeated HEGLER'S work and found no increase in mechanical tissues even in the plants with which HEGLER worked.

HIBBARD (10), also working along the same lines, found no increase in mechanical tissues with tension except in one plant (*Vinca*), where a slight increase was noted.

The work of VÖCHTING (23) upon *Helianthus annuus*, of WIEDERSHEIM (25) upon woody stems, and of KELLER (11) upon fruit stalks has likewise shown no response due to tension.

Later work by BORDNER (3) seems to show an actual increase in breaking strength and in amount of mechanical tissue in the several species with which he worked. This investigator, by the

use of a large number of individuals in each experiment, has, we believe, demonstrated that there is an actual response of the plant to tension, by which stronger tissues are laid down and the tensile strength of the part under tension increased, though not to such an extent as HEGLER's results seem to show.

Another line of investigation on the effect of tension has been followed in a comparison of the cells on opposite sides of a stem which has been prevented, by weighting, from responding to a heliotropic or negative geotropic stimulus (BALL **1**, pp. 326 f.). In this case a thickening of cell walls occurs on the convex or upper side of the stem, which has been believed by some to be due to a state of tension. A similar thickening occurs (BALL **1**, p. 339) on the upper side of a stem in a plaster cast placed horizontally, also in the concave portion of a stem which has formed a curve. In the last case cited, BALL demonstrated that no increase in breaking strength of the stem took place, a fact which he attributes to the concave side being built up at the expense of the convex side. This is substantiated by the investigations of PENNINGTON (**16**) on the effect of compression on plant stems, where he finds a reduction in the thickness of cell walls due to compression.

While a number of investigators have thus studied the effect of mechanical strain upon tissues in stems, the investigations on tendrils have been almost exclusively for the explanation of external movements, such as the cause of coiling, etc. (For explanation of external phenomena see FITTING **7**, DEVRIES **6**, and MACDOUGAL **13**.) The anatomical structure has been worked out in a comparative manner by MÜLLER (**14**) and WORGITZKY (**26**), but only by the latter writer was the tendril treated in relation to its function.

DARWIN (**5**, p. 58) noted that in petiole climbers the petioles are thickened from contact, and TREUB (**22**, p. 65) found marked changes in the anatomical structure of the portion of the petiole in contact, consisting in a greater development of the mechanical system, which is borne out in a general way by the later work of VON DERSCHAU (**24**).

MÜLLER (**14**), in his study of the tendrils of the Cucurbitaceae, found that contact produced earlier and greater lignification of sclerenchyma in the free portion on the under side (p. 127).

WORGITZKY (**26**) is the only investigator who tested the breaking strength of tendrils with and without a support. He noted that a *Passiflora* tendril which had grasped a support broke at 600 grams, while one free from a support broke at 350 grams. A tendril of *Cucurbita Pepo* likewise seemed to show greater strength of tissues when a support had been grasped. Even supposing that these tendrils tested were of the same age (which is not stated by the author), these data have little value in the present paper, since it is not known whether the tendrils with a support were under tension or contact alone. WORGITZKY found in his anatomical study that marked anatomical differences come in with the grasping of a support. As to the cause of these anatomical differences, none of these investigators have written. VON DERSCHAU (**24**) by an ingenious method sought to separate the influence of tension from that of contact in his experiments with petiole twiners, by attaching a clamp to the leaf and suspending a weight thereon. Contact alone was secured by allowing a petiole merely to twine around a stick. It was found that contact alone or tension alone, gradually increased, called forth a greater development of mechanical tissue, a still greater increase taking place with the combination of both factors. It seems doubtful, however, whether the contact stimulus was avoided by this method of experimentation.

Methods

Experiments were conducted in the greenhouse under very constant and favorable conditions for growth.

Special care was taken to secure proper controls, since among tendrils, as throughout the plant kingdom, much variation occurs in size and vigor of individuals; however, it was found upon investigation that tendrils on the same vigorous vine within two or three internodes do not vary to an appreciable amount; this conclusion was based upon a comparison, by means of camera drawings, of sections of the ring of mechanical tissue of several tendrils on the same vine and on different vines, all under the same conditions (a weight of 15 grams) and all of the same size and vigor. These drawings show the areas of mechanical tissue of tendrils near each other on the same vine to coincide practically,

while those from different vines have different areas. The reliability of this method of securing controls is also shown by a comparison of the breaking strength of tendrils from the same and from different vines, which shows tendrils on the same vine under the same conditions to correspond quite closely in tensile strength.

Measurements were also taken to secure proper controls, but it was found that healthy tendrils on the same vine varied only slightly in rate of growth, and were ready for contact at approximately the same age. As the time when the tendril is most suitable for contact can be judged within 24 hours, and since the time between the maturing of tendrils on successive nodes is quite constant, a very uniform method of starting the experiment on each tendril was obtained. Moreover, when tension was applied, a certain scheme for weighting was used, to secure gradually increased tension at the same rate in each case. The experiment on each tendril was closed at exactly the same length of time from the date when it was begun, and note of weather conditions was taken during the time of experiment.

Tendrils which had been under experiment were compared by two methods: (1) by their breaking strength, and (2) by their anatomical structure. The breaking strength was obtained by wrapping the extremities of the portion to be tested with damp cotton dipped in plaster of Paris; each end was then fastened between a pair of wooden blocks, made for the purpose, which were screwed tightly together; this preparation was then placed on a machine for breaking; one of the blocks was connected to a rod on which a thumbscrew was turned, to secure gradually increasing tension; the other block was connected to a spring balance from which was read the degree of tension at which the tendril broke. A straight portion of the tendril was always taken for testing. When the break occurred at the place of attachment of the tendril, the result was thrown out.

Cross-sections of tendrils were made and microphotographs taken at a magnification of 100 diameters. This shows well the form and arrangement of the mechanical tissues. Camera sketches of the area of mechanical tissue were also made and compared with microphotographs of the same tendrils in the study of the cross-

sections. Thickness of walls was also measured with the camera lucida, and special note was taken in the anatomical study of the number and size of cells in the ring of mechanical tissue.

Tendrils were placed under tension of different degrees by causing a tendril to coil about a short piece of reed supported at either end by a wire, to which was attached a cord and the same run over a pulley, the weight desired being attached to the other end of the cord. Contact without tension was obtained by the use of a counter-balance. Unless otherwise stated, tension and contact were always secured by this means.

When a ligature was used to secure tension, a strip of soft cotton flannel was wrapped about the tendril, and the string secured by a series of hitches only tight enough to grip the tendril firmly. This was found not to injure the tendril in the least, since it develops a soft cushion of tissue at the place of contact; moreover, in *Passiflora* a greater number of xylem cells is always produced at the place of contact, which tends to prevent any injury to the tissues. Sections taken at the place of ligaturing, except where too heavy weighting was introduced, showed the mechanical tissues to be normal, and the outside diameter often greater at this place than either immediately above or below.

A series of experiments was set up to determine the effect of ligaturing on the development of mechanical tissues. Two sets of *Passiflora* tendrils were used for comparison; in the one set attachment was secured by allowing the tendril to coil about a support as already described, in the other a ligature was tied about the contact portion of the tendril, and the same amount of tension was applied to each. Breaking strengths of these tendrils are given in table I.

These results show a slightly greater average breaking strength in the ligatured tendrils over those coiled about a support; this increase is evidently due to individual variation. These experiments and observations on ligaturing show clearly that the tendril suffers no injury whatever from this treatment. When ligatures were used to eliminate the contact stimulus, they were applied in some experiments one day, in others two days after the time when the tendrils were most sensitive to contact. Carnoy's fluid (4)

was used for killing and fixing material, as this preparation penetrates woody tissues very rapidly. Sections were stained in

TABLE I

DURATION OF EXPERIMENT 32 DAYS; FINAL WEIGHT USED 20 GRAMS

	With support	With ligature
1	1050 grams	1200 grams
2	1050	975 1265
3	1275	1475
4	1350	1250
5	1425	1475
6	750	775 925
7	820	925
Average	1103 grams	1140.5 grams

anilin safranin in order to bring out clearly the lignified tissues. Permanent slides were made by mounting in Canada balsam.

Further detailed methods are given in each experiment.

Experimental work

DETAILS OF EXPERIMENTS

1. *Tendril free, with contact, with contact and tension.*—In the first series of experiments, tendrils were placed under the following three conditions: (1) without any contact whatever, (2) with contact alone, and (3) with contact and tension. In the last case, contact was secured by allowing the tendril to twine about a support as before described. The three tendrils of each set to be compared were chosen from the same vine according to the methods previously given. A final weight of 20 grams was chosen after a few preliminary trials, which showed that 20 grams was the highest weight which could be used on the average *Passiflora* tendril without producing a weakening effect. The breaking strength of these tendrils is given in table II.

These results show clearly an increase in breaking strength due to contact, and a still greater increase when tension is applied. We have yet to determine, however, whether this increase with tension is due to the longitudinal pull or to increased contact,

that is, to the increased radial pressure of the contact portion against the support, due to the pull of the weight.

TABLE II

DURATION OF EXPERIMENT 32 DAYS*

Free	Contact	Contact and tension (20 grams)
I_1—112 grams	I_2— 775 grams	I_3—1425 grams
G_1—150	G_2— 725	G_3—1170
	E_2— 850	
E_1—125	E_3— 675	E_4—1050
F_1—450	F_3—1040	F_4—1275
H_1—740	H_2—1270	H_3—1350
D_1—390	D_2— 850	D_3—1095
	B_1— 900	B_2—1050
	A_2— 575	A_3—1200
K_1—120	K_2— 375	K_3— 400
M_1—152	M_3— 575	
N_1—240	N_2— 650	N_3—1275
L_1—100	L_2— 850	
	L_6— 660	
J_1— 75		
J_5—155	J_2— 450	J_3— 700
U_1—130	U_4— 970	U_3—1125
	V_1— 450	V_5—1110
W_1—185	W_2— 365	
X_1— 40	X_2— 575	
C_1—190		
C_2—110	C_4— 408	C_5— 905
C_3—145		
P_2—100	P_1— 760	
	R_2— 580	R_1— 705
	O_2— 420	
O_1— 85	O_7— 390	O_8— 660
	Q_1— 305	
	Q_7— 490	Q_8— 630
Average (20 tendrils), 190	Average (26 tendrils), 651	Average (17 tendrils), 1007

* Capital letters denote vines, subscripts denote tendrils, which were numbered consecutively on the vine from below upward.

2. *Middle third.*—To determine the influence of tension alone the following method was devised. In the one set a ligature was tied at the distance of a third the length of the whole tendril from the tip, and another the same distance from the base (fig. 1). To the distal ligature tension was applied by running the cord over a pulley, and from the proximal ligature a cord ran to the stem, which was made taut, so as to relieve the basal third of the

tendril from any strain. In the other set, the distal ligature was placed the same as the corresponding one in the first set, and a second ligature placed just below this. To the distal one tension was applied, and from the proximal one a cord ran to the stem, relieving the basal two-thirds of tension. By this device we have one tendril with the middle third under tension, the other with this portion not under tension, and the factor of contact the same in both, except that the proximal ligature is in a more sensitive part of the tendril in the second preparation than in the first, which would tend toward a greater development of mechanical tissue in the second preparation.

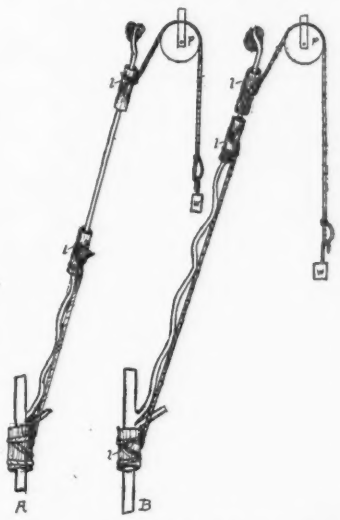

FIG. 1.—*A*, tension-tendril; *B*, tension-free tendril; *p*, pulleys; *l*, ligatures; *w*, weights.

Breaking strengths of the middle third of these tendrils are given in table III.

TABLE III

PERIOD 28 DAYS; FINAL WEIGHT 20 GRAMS

Under tension	Tension-free	Under tension	Tension-free
A_5—1100 grams	A_3— 875 grams	F_4—1275 grams	F_3— 950 grams
A_6— 950	A_5— 675	F_5—1090*	F_6— 900
A_8—1000	A_7— 700†	F_7—1200	F_8— 825
B_3—1475	B_2— 875	G_1—1625	G_2—1020
[B_4— 900]*	B_5— 900	G_3—1775	G_4—1000
B_7—1090	B_6— 650	G_5—1175*	G_6—1000
B_8— 900	B_9— 890	[G_7—1300]‡	
C_2—1075	C_3— 650	G_8—1535	
C_4—1075	C_5— 575	G_9—1425	G_{10}—1315†
C_7— 975	C_6— 725	G_{11}—1650	
D_4—1200	D_3— 625	H_2—1075	H_1— 735
D_5—1875	D_6— 850	H_3—1370	H_4— 865
D_8—1085	D_7— 710	H_5—1300	H_6—1685†
F_1—1325	F_2—1100		
		Average 1239	Average 862

* Broke at ligature. † Had to be broken close to base. ‡ Tension—coiled about a support.

With but one exception (H_6), these results show uniformly a decided increase in breaking strength of those under tension. The exceptional breaking strength of this tendril is partly accounted for by the fact that the break occurred in the basal third, which has a greater development of mechanical tissues. We can only conclude from these results that tension does produce greater strength of tissues in the middle third of the tendril.

3. *Basal third.*—The next experiments were for the purpose of determining the effect of tension on the less sensitive basal or proximal third of the tendril by the same method, only one ligature being used on the one under tension, however (fig. 2), and a counter-weight (*cw*) used in the one tension-free, instead of the cord being tied back to the stem. Breaking strengths of the basal third in the two sets of the tendrils are given in table IV.

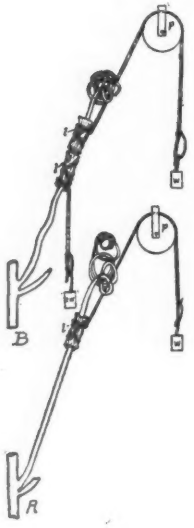

FIG. 2.—*A*, tension-tendril; *B*, tension-free tendril; *p*, pulleys; *l*, ligatures; *w*, weights; *cw*, counter-weight.

These results show no decided difference in strength between the two sets of tendrils compared as in the preceding experiments on the middle third. However, it is quite possible that the increase in strength of the "tension-free" tendrils in this experiment compared to the last is due to the tension stimulus received by the portion between the two ligatures, this stimulus being conducted through the tissues to the basal part; the contact stimulus is also greater here, due to the *two* ligatures compared to *one* in the tension tendril.[2]

In order to eliminate these additional stimuli the following method of experimentation was devised. Two loops of cord were made about the tendril not under tension at the same distance from the base as was the

[2] A study of sections of these tendrils (see below, under anatomical study) shows that these stimuli causing the formation of more mechanical tissue are actually transferred in the manner here stated.

TABLE IV

Series I

PERIOD 66 DAYS; FINAL WEIGHT 200 GRAMS

Under tension	Tension-free
A_4—1925 grams	A_5—1125 grams
A_8— 925	A_9—1450
B_3—1675	B_4—2150
B_7—1475	B_8—1775
G_4—2125	G_5—2000
G_8—1375	G_9—1550
Average 1583	Average 1675

Series II

PERIOD 32 DAYS; FINAL WEIGHT 50 GRAMS

Under tension	Tension-free
A_6—1890	A_7—1800
B_5—1490	B_6—1775
C_4—1260	C_5—1360
D_4—1150	D_5—1500
G_6—1600	G_7—1710
I_4—1930	I_5—1690
J_3—1270	J_4—1175
Average 1513	Average 1573

Series III

PERIOD 32 DAYS; FINAL WEIGHT 20 GRAMS

Under tension	Tension-free
C_7—1290	C_6—1440
E_6— 890	E_7— 900
F_6—1125	F_7—1160
	H_6—2100
H_5—1725	H_7—1965
I_7—1650	I_6—1600
J_6—1190	J_5—1215
O_5—1100	O_4—1400
O_6—1210	O_7—1200
Q_4— 900	Q_5— 775
S_4—1420	S_5—1220
D_6—1275	D_7— 985
Average 1261	Average 1260

ligature in the one under tension; these loops were so arranged that they acted against each other (fig. 3), so that when the upper one was run over a pulley and a weight attached and a like weight hung on the one below, a pressure equal to the weight used was exerted radially upon the tendril. In order that no injury might be done to the tendril, three lengths of soft cotton twine were placed lengthwise to the tendril, so that they lay between the loops and the tendril; this served well to transmit the pressure to the surface of the tendril. In only a very few cases was the tendril injured by this means. Where such injury occurred, the tendril was thrown out of record. In both cases attachment was made to the tendril slightly below that in the preceding experiment, so that it was just within the proximal third of the tendril, to avoid the contact stimulus as much as possible, since the sensitiveness of the tendril diminishes rapidly toward the base.

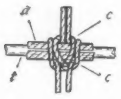

FIG. 3.—*t*, tendril; *c*, loops of cord; *a*, lengths of soft twine to protect tendril from injury.

Weights were added as in the preceding experiment. Breaking strengths of these tendrils are given in table V. Four tendrils in this series were allowed to grow without any contact whatever, to determine the effect of contact-pressure on the basal portion of the tendril, and are included in this table; likewise, one tendril which had a ligature placed similarly to those in the first two columns but without tension or contact-pressure.

These results are very different from those in the last experiment, and seem to verify the inferences made as to the real cause of the unexpected increase in strengthening tissues in the tension-free tendrils in the preceding experiments. That this increase did not take place in the "tension-free" tendrils in the experiments on the middle third is no doubt due to the fact that the part under tension in this case was in the upper or contact portion of the tendril, which is not so sensitive to the tension stimulus. "Tension-free" tendrils show an increase in breaking strength over "free" tendrils, while those under tension show a much greater tensile strength. This must mean that tension in the lower part of the tendrils is effective in giving greater strength to that portion.

Contact-pressure in this case seems to play a comparatively small part.

TABLE V

PERIOD 37 DAYS

UNDER TENSION			TENSION-FREE			CONTACT-FREE	
Tendril	Final wt.	Breaking strength	Tendril	Final wt.	Breaking strength	Tendril	Breaking strength
A_2	100 grams	460 grams	A_1	100 grams	350 grams	A_5	115 grams
			A_4	20	190	A_6	120
C_1	100	1150	C_2	100	300		
C_4	20	1160	C_3	20	300		
C_5	20	1075	C_6	20	235	[C_7	215]*
D_2	100	975	D_1	100	325		
			D_4	20	210		
D_6	20	1385	D_5	20	275		
			D_7	20	275		
E_3	20	780	E_1	50	350		
			E_4	20	185		
			F_1	70	235		
G_1	100	1200	G_2	100	350		
G_4	20	1465					
G_5	20	111	G_3	20	210		
G_7	20	12400					
			H_2	50	225		
H_4	20	1100	H_3	20	300	H_7	160
H_5	20	925	H_6	20	190	H_8	140
Averages		1073			265		134

* This tendril had ligature only.

4. *Pressure.*—Another method of separating the influence of contact from that of tension consisted in allowing the tendril to twine about a piece of pure rubber tubing, which is very elastic, and after the coils had become firm, to apply pressure inside the tubing by means of a column of mercury. A single thickness of pure cellulose paper was wrapped about the tube to prevent any poisonous effect upon the tendril. In order that the tendril might grip the tubing tightly, so that the pressure could be applied effectively, the tubing was doubled upon itself radially and fastened by a few turns of cord; as soon as pressure was wanted, this cord was cut, which put the tendril and rubber in close contact, so that very little of the pressure from the column of mercury would be taken up by the rubber. The effectiveness of this method was aided by the contraction which takes place in the tendril after the coils have formed (FITTING **7**). It was calculated that a height of

only about 10 cm. of mercury was necessary to secure the same amount of radial pressure that is exerted on the contact portion when 20 grams tension is applied to the tendril with the contact portion coiled about a support, due allowance being made for the pressure taken up by the resistance of the rubber tube.

Since, however, in spite of the care taken to secure a close contact between tendril and tube, the amount of pressure which was actually exerted upon the tendril was dependent upon how closely the tendril had coiled about the tube, only relatively high pressures were used, which were for the purpose of determining the effect of pressure alone upon the tendril. A small amount of pressure was applied at first and gradually increased. The tensile strength of the whole tendril was determined in all experiments on the effect of pressure, to see whether an actual increase in the strength of the tendril had occurred. The break occurred, with a very few exceptions, in the middle third.

TABLE VI

PERIOD 28 DAYS

INCREASED PRESSURE			NORMAL PRESSURE	
Tendril	Hg. height	Breaking strength	Tendril	Breaking strength
A_2	55 cm.	1085 grams	A_1	785 grams
E_4	30	1775	E_2	975
			E_3	1025
I_2	22	1150	I_1	715
I_3	30	950		
L_2	20	715	L_1	615
L_3	30	960	L_5	625
M_4	45	900	M_3	575
M_5	30	720		
M_6	30	1160		
N_3	30	915	N_5	725
N_4	30	850		
V_3	30	700	V_4	500
Averages		990		727

The breaking strengths as shown in table VI show an undoubted increase in the strength of tendrils with increased radial pressure. That the increase was small in some cases may be due to the failure of the tendril to coil about the tubing securely.

That longitudinal tension may enter into this experiment is quite possible; however, in many tendrils in this experiment where pressure was applied, the contact with the rubber tubing was so close as to permit of a seemingly small amount of longitudinal stretching. That this increase was not in the main due to longitudinal tension may be inferred by a comparison with the results in table VII.

TABLE VII

PERIOD 28 DAYS

PRESSURE WITH WEIGHT			CONTACT PRESSURE	
Tendril	Final wt.	Breaking strength	Tendril	Breaking strength
H_1	15 grams	625 grams	H_2	520 grams
K_1	20	600		
K_2	15	685	K_5	740
K_4	5	775		
L_1	20	540		
L_3	20	690	L_2	650
L_4	15	875	L_5	675
M_5	20	875		
M_6	20	600	M_1	600
M_7	15	975		
N_1	20	775		
N_2	20	935	N_5	675
N_3	15	675		
S_1	20	790	S_5	575
S_2	15	890		
Averages		745		634

In order to determine how great a part pressure actually has in the formation of mechanical tissue in tendrils, weights were placed upon the most sensitive part of the tendril, the latter being supported by a small platform suspended from above by a cord. Weights were added exactly the same as when tension was used in the former experiments, and the same length of the tendril was placed under pressure as was calculated to be under pressure in the tension experiments.

The breaking strengths of these tendrils as given in table VII show a slight increase over those tendrils which had contact alone. We infer from this that the additional radial pressure caused by an amount of tension equal to 20 grams does not greatly increase

the strength of the tendril. This may be explained by the supposition that a weight of 20 grams does not exert a pressure much greater than is caused by the contraction of the contact portion of the tendril when coiled about a support.

Ligatures were also tied about tendrils in different regions to determine the effect of contact in a more and in a less sensitive part of the tendril. The effect of these ligatures in regions *a* and *b*, respectively, upon the breaking strength is shown in table VIII; *a* was about one-third the length of the whole tendril from the apex, and *b* the same distance from the base of the tendril.

TABLE VIII

PERIOD 32 DAYS

LIGATURE AT *a*		LIGATURE AT *b*	
Tendril	Breaking strength	Tendril	Breaking strength
B_7	230 grams	H_8	590 grams
D_8	550	H_{10}	310
D_9	510	H_{11}	160
I_5	490	K_4	140
I_6	650	K_5	225
J_2	650	K_6	260
J_4	700		
J_5	665		
L_3	510		
M_3	600		
M_4	750		
Averages	573		281

These results show that a ligature placed in a more sensitive region (*a*) calls forth a greater formation of mechanical tissue than when placed in a less sensitive region (*b*). This accords with the former inferences made in experiments on the middle third and basal third.

RESULTS IN BREAKING STRENGTH

The following conclusions may be deduced from the foregoing results in breaking strength of tendrils:

1. Contact alone plays an important part in giving strength to the tendril.

2. When contact is increased by pressure, a further increase in the strength of the tendril is produced.

3. When the factor of tension is added to that of contact, a still greater strength results to the tendril.

ANATOMICAL STUDY

1. *General anatomy of the Passiflora tendril.*—A cross-section of a tendril of *Passiflora caerulea*, in accordance with the observations of MACDOUGAL (**13**) and WORGITZKY (**26**), reveals the following tissues, beginning at the outside: epidermis, collenchyma, thin-walled parenchyma, bast, xylem (which forms a complete ring, due to secondary growth), and in the center pith. In mature tendrils the pith entirely fills the central part except in the basal portion, where there is a central cavity within the pith. The walls of the xylem and bast are much thickened, and so are (as WORGITZKY has noted, p. 34) the walls of the pith. The xylem becomes lignified, also the bast somewhat, and, as MACDOUGAL observed, lignification extends to the pith also.

At the base the arrangement of tissues is very nearly radial, but in the portion in contact a marked dorsiventrality is seen, which is due principally to the development of the xylem to a much greater extent on the side in contact. A section midway between the apex and base of the tendril shows a slight dorsiventrality, a somewhat greater amount of xylem being formed on the concave side.

2. *Study of sections; experiments on entire tendril (free, with contact alone, and with contact and tension).*—Sections were made through the middle of the tendrils, as this was found to be the place at which the break invariably occurred in these experiments. Tendrils as near as possible to the average breaking strength were taken for sectioning. A comparison of sections reveals the following.

The mechanical tissue of the free tendril is limited to a small area of xylem on the concave side, and only the four primary bundles on the opposite side. The xylem cells are quite thin-walled compared with the xylem of the other tendrils in this experiment, and the primary bundles of the opposite side are

composed of two or three slightly thickened vessels. In this region only a few bast fibers are present, which are very small; very little pith is present, which lines a central cavity. Toward the base a complete ring of thin-walled xylem and pith is formed.

Sections of those tendrils under contact and under tension show the normal complete ring of mechanical tissue and central thin-walled pith. At the first examination of these sections, little difference could be seen in structure or areas of mechanical tissue, and camera sketches show no difference in thickness of walls of the xylem, though the greater part of those under tension had a tensile strength 50 per cent higher than those with contact alone. A closer examination of the sections with the aid of microphotographs and camera sketches shows that while the xylem areas are approximately the same in both, in the one where tension had been introduced the walls of the pith cells have become much thickened, while in the one with contact alone they are quite thin-walled. This thickening of walls takes place usually throughout the whole area of the pith of the tendril under tension, while in the one which had been under contact alone the pith is thin-walled throughout. It is worthy of note also that in sectioning, the ones under tension were much harder to cut through, which is no doubt due to a difference in density of cell walls.

3. *Study of sections; experiments on middle third.*—Examination of sections of those tendrils where the middle third was (1) with and (2) without tension shows the diameter of mechanical tissue to be much greater in the latter, which accounts for the greater outside diameter usually found in these tendrils. This seemingly greater area of mechanical tissue in the tendril grasping a support but not under tension is somewhat surprising when we consider that those under tension had a breaking strength nearly 50 per cent higher. This increased strength with tension is at least partly accounted for by the fact that the pith walls in the tension-tendril are thickened (very similarly to those in the preceding experiment under tension), while in the one not under tension all the pith is thin-walled. In order to be certain that this thickening of the pith is constant with those under tension, sections of more than 30 tendrils in this experiment were studied

and compared, each being labeled so that it could not be told during the examination which was from a tension and which from a tension-free tendril. In every case it was possible to decide with certainty which one had been under tension from the appearance of the pith, and each decision was later verified by referring to the record. The walls of the pith were in most cases thickened in a marked manner to the very center. Measurements with a planimeter show the tension-free tendril to have the greater area of xylem, while the tension-tendril has the greater amount of mechanical tissue when thick-walled pith is included. Comparative areas were found to be as follows:

	Xylem	Pith (thick-walled)	Total
Under tension	2.61	2.78	5.39
Tension-free	4.51	....	4.51

In these experiments, as in the others where tension was used, a marked characteristic of the sections of tension-free tendrils was that the pith was found more or less displaced by the process of sectioning, while in those from tension-tendrils the pith held its shape as if firm.

In all these tendrils it was noted that tendrils which had been under tension were more rigid and much harder to cut through than those free of tension, as noted in the preceding experiments.

Sections were taken also through the basal third of these same tendrils. A close resemblance was found between sections in these two regions (middle and base) in the same tendril. In the basal part of the tendril in which the middle third had been under tension, the diameter of the mechanical tissue is smaller and the pith thick-walled throughout, while in the tendril tension-free the pith is very thin-walled in the corresponding region. This shows remarkably how the stimulus for growth may be transferred through the tissues to a part which has not received the stimulus directly, since the basal part in neither case in these experiments was under tension.

4. *Study of sections; experiments on basal third.*—Sections of tendrils in which the basal third was tested were studied with the

view especially to ascertaining the cause of the difference in results obtained in breaking strength under the two different methods of experimentation (see tables IV and V). Sections of tendrils in the first set of experiments (where two ligatures were used in the one not under tension) showed the ring of mechanical tissue in the one not under tension to have a greater outside diameter than that in the one under tension. Xylem and thickened pith are present in both tension and tension-free tendrils. A well marked difference could be observed, however, between the amounts of xylem and thickened pith in the two sets of tendrils. In the one not under tension xylem was present in greater quantity than in the one which had been under tension, while in the tension-tendril thickened pith was in much greater quantity than in the one without tension. In a typical tendril the comparative amounts of xylem and thick-walled pith were as follows:

	Xylem	Pith thick-walled	Pith thin-walled	Total mechanical tissue
Under tension	6.0	4.7	(1.7)	10.7
Tension-free	7.2	1.8	(3.6)	9.0

The fact that, nothwithstanding the smaller area of mechanical tissue, the breaking strength of the ones not under tension was practically the same as in those under tension, is no doubt due to the fact that much of the thick-walled pith in the tension-tendril does not possess as thick walls as does the xylem; hence does not give as much strength to the tendril as does the latter. An examination of sections in the second series of experiments on the basal third, where contact-pressure was applied to the tension-free tendril by means of two loops of cord pulling against each other, shows a very different appearance from that just described when tension and tension-free tendrils are compared. In this case the area of xylem is practically the same in both, being about equal to the amount found in those under tension in the above experiments on the basal third; in the ones not under tension the pith is thin-walled throughout, is small in amount, and has a large cavity in the center; in the ones under tension the pith is much

thickened, is larger in amount than in the last, and the central cavity is much smaller.

If we now compare the structure of the tendrils in the two methods of experimentation, it becomes very evident that the additional amount of xylem in the tension-free tendrils (as compared to the tension-tendrils) of the first set is due to the extra contact-pressure introduced, and the thick-walled pith found in the same tendrils, which has not before appeared in tendrils except when tension was introduced, is due to the stimulus of tension conducted to the basal part from the portion in tension between the two ligatures. That this thickening of the pith which was caused by only a small portion of the tendril being under tension did not appear in the former experiments on the middle third of the tendril is no doubt due to the fact that the tension in the latter case was in the contact portion of the tendril, which is not so sensitive to the stimulus of tension as is the lower two-thirds of the tendril.

5. *Study of sections; experiments on contact portion.*—Examination of sections through the contact region of tendrils which had been put under (comparatively) great pressure by a column of mercury failed to detect any difference in anatomical structure when compared with those which had been in contact only. Sections through the middle of the tendrils, however, where there was no tension and where the break usually occurred, show marked differences between the two sets of tendrils in the amount of xylem present. The area of xylem in the ones which had been under pressure, in an average tendril, was approximately twice as great as the area of xylem in the ones which had been in contact only. No differences in the pith could be detected; it was thin-walled alike in both sets of tendrils.

In those cases where a pressure of 20 grams was obtained by laying a weight on the tendril, no difference could be observed between these tendrils and those under mere contact, though the former had a slightly greater average breaking strength. Both had the usual ring of xylem and the pith was thin-walled.

Sections were not made of tendrils which were ligatured in different regions.

SUMMARY AND CONCLUSIONS

These changes in structure under changing conditions which were observed upon a number of tendrils in each condition and were found constant in each case, almost without exception, have but one meaning to the writer. In experiments where tension was introduced, the marked increase in thickness of pith walls, which was found only when the factor of tension was present, can be explained only by the theory that this thickening is due to the longitudinal pull on the tendril, by which the tensile strength of the tendril is increased.

That pith may serve as mechanical tissue is a thing for which no evidence has heretofore been offered. DEBARY says (*Comp. anat.*, p. 533):

> The only demonstrable change in the pith during the phenomena of secondary growth is that it sooner or later, rapidly or slowly, dies off and dries up. The possibility of a change in the pith caused directly by the growth in thickness is not, indeed, excluded a priori. For . . . . the increasing pressure . . . . exercised on the pith [by the xylem] may lead to anatomical changes in the latter. In what cases and in what form such changes may possibly take place are questions which have not been investigated, and to the solution of which there is scarcely any safe clue; the possibilities will not be discussed here.

WORGITZKY noted a thickening of the walls of the pith in the tendrils of *Passiflora caerulea*, *P. triloba*, and *P. quadrangularis*, "after a support had been securely grasped." He also adds "the purpose or cause of this was not found"; and MACDOUGAL noted that lignification extended to the pith in the basal part of tendrils of *P. caerulea*.

In view of the results of observations and experiments presented in this paper, I maintain that this thickening of the walls of the pith cells in *Passiflora caerulea* is an adaptation, where tension acts as an irritation-stimulus, for producing greater tensile strength to the tendril where needed.

In the series of experiments on the contact portion, the great increase in xylem below the part in contact, accompanying the increased pressure, leads to the conclusion that contact-pressure has a marked effect upon the structure of the tendril. That a pressure of 20 grams does not cause a decided increase in xylem

may be explained if we assume that the pressure exerted on the support by the coils of the part in contact which contract after grasping the support is equal to 20 grams for the whole area in contact. No constant change could be noted in the amount of bast present under these varying conditions, except that very little could be found in the free tendrils. As the bast plays only a comparatively small part in the *Passiflora* tendril, this tissue was not taken into consideration.

The conclusion from these anatomical studies on *Passiflora* can only be that contact-pressure causes a greater formation of xylem in the tendril, while longitudinal tension causes a thickening of the walls of the pith whereby greater tensile strength is secured.

General conclusions

To return to the problem of the present paper (as given in the introduction), my conclusion in regard to *Passiflora caerulea* is that those tendrils which function to support the plant, that is, that are under the influence of contact and tension, possess a greater breaking strength than those which have grasped no support (see table I).

The cause of this greatly increased strength, as shown by the experiments on the middle third, basal third, and contact portion, and a study of sections of the same, is clearly due to a combination of the two factors contact and tension, the cells of the xylem being increased both in number and in thickness of walls by the former stimulus, and the walls of the pith much thickened by the latter. Comparing the values of these two factors in the formation of mechanical tissue in the *Passiflora* tendril, I conclude that contact plays by far the most important part, though the strength of the tendril may be still more increased (even 50 per cent) by the additional factor of tension.

As to the influence of contact upon the formation of tissues, we have had a large number of observations, not only in regard to tendrils, but also in regard to plant tissues in general.

That tension also may act as a stimulus, and that thereby stronger tissues are built up in the plant, has been shown by the experiments of BORDNER (**3**); this is substantiated by the observa-

tions and experiments presented in this paper. This accords with the observations of HEGLER (**8**) that the retarding effect of tension is closely related to the daily periodicity of growth in length, which seems to show that tension acts as a true stimulus upon the plant cell. As to the exact method by which this increase and strengthening of tissue takes place we are unable to say, since we know very little, as yet, of the nature of the changes taking place in the cell and especially in the cell wall, under the influence of tension.

It seems not unlikely that this increased growth is due to increased hydrostatic pressure in the cell, since HEGLER found a higher hydrostatic pressure in plants which had been under tension than in plants growing normally (**7**, p. 416).

The state of tension in which the cell wall might be, may act as an irritation-stimulus for the laying down of more tissues either by apposition or intussusception; here, however, we should have to assume the cell membrane (at least in part) to be composed of living protoplasm, for which assumption we have no well founded evidence (see PFEFFER **18** [EWART transl.], **1**:485).

As to why this thickening in *Passiflora* did not occur in the xylem also under the influence of tension, we are unable to say; this difference in response is probably due to fundamental differences in these tissues.

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A COMPARISON OF THE RATES OF EVAPORATION IN CERTAIN ASSOCIATIONS IN CENTRAL ILLINOIS[1]

HENRY ALLAN GLEASON AND FRANK CALEB GATES

(WITH SIX FIGURES)

During the session of the Biological Summer School of the University of Illinois, held at Havana, Ill., during June and July 1910, a series of measurements of the relative rates of evaporation within certain plant associations was made. In view of the growing interest in the study of evaporation and its relation to vegetation, the results obtained are here presented.

The greater part of our knowledge of evaporation in relation to vegetation has been given to us through the work of LIVINGSTON and TRANSEAU. One of the most suggestive papers is that of TRANSEAU,[2] in which he determined the relative rates of evaporation for a number of habitats about Cold Spring Harbor, Long Island, N.Y. He has summarized his results in a diagram which clearly shows the marked difference in the amount of evaporation in areas close to each other but differently vegetated. While TRANSEAU worked with habitats, as he expresses it, in the work at Havana certain definite plant associations were selected in which to determine the rate of evaporation.

Havana is located on the east bank of the Illinois River in central Illinois. The climate may be briefly characterized by the following statements: an average temperature during June and July of about 24° C., with warm nights and hot days, and a yearly rainfall of about 90 cm., of which considerably more than half falls during the growing season. Strong winds are frequent, as is usually the case in the central states. Except on the alluvial river bottoms, the soil of the area is sandy with a slight admixture of humus. Most of the area was originally occupied by associations of the Prairie

[1] Contribution no. 125 from the Botanical Laboratory of the University of Michigan.

[2] TRANSEAU, E. N., The relation of plant societies to evaporation. BOT. GAZ. 45:217–231. 1908.

Province, but the climatic dominance of the associations of the Deciduous Forest Province is now gradually asserting itself wherever conditions are not interfered with by man. The climax type of vegetation for this part of Illinois, the *Acer saccharum* association, does not occur in the immediate vicinity, although it is present on clay and loess bluffs on the opposite side of the river.

The principal object of the investigation was the determination of the relative amounts of evaporation in certain well marked associations whose successional relations were clearly evident, in order to correlate the phenomena of succession and evaporation. A minor object was the comparison of evaporation in two areas with the same dominant vegetation, but with different secondary species. The results obtained were even more striking than had been anticipated.

The atmometers used were porous clay tubes, of the model recommended by TRANSEAU, about 30 cm. long and 2 cm. in diameter. The tubes were inserted into bottles through holes in the corks, and were then sealed with red sealing wax to prevent the entrance of rainwater and the loss of water by evaporation. A small S-shaped groove on the side of the cork permitted the equalization of the atmospheric pressure within the bottle. Reading the instruments immediately before and after heavy rains indicated that the arrangement was water-tight. The instruments were filled with distilled water, and to each 250 cc. was added one drop of formalin to prevent the growth of organisms. According to LIVINGSTON[3] the addition of formalin is not recommended in studies of absolute values of evaporation. Since this study was concerned with relative values only, and since all the instruments were treated alike, the slight effect of formalin is without significance. The instruments were set up and allowed to run for three weeks before the field records were taken, to insure the thorough saturation of the clay tubes. Each bottle was marked just below the cork, and was refilled by pouring in water from a graduate up to the mark. The readings were estimated to be correct within 0.5 cc. All the instruments were exposed together in the open air for 93 hours for standardization. Eleven instruments were then exposed in the association selected, while a twelfth, arbitrarily chosen as the stand-

[3] Plant World **13**:118. 1910.

ard, remained in its original location. Readings in the field were continued for 23 days, and then all the instruments were again standardized for 93 hours in the original location. Readings of the standard were taken daily, while those in the field were read at intervals of one to four days. Since the purpose of the work called for the total amount of evaporation rather than the daily fluctuations, the observed amounts of evaporation from each instrument were added, and the total amounts reduced to terms of the standard instrument by multiplying by the factor obtained in the two standardizations. The results are therefore directly comparable, and have been plotted in the accompanying diagram (fig. 6). Since they are not absolute values, they have been expressed in terms of the evaporation from the standard instrument, which is here designated 1.00.

Two atmometers were located in each of five distinct associations, and one other was set up on the sandy beach of Quiver Lake. Four of the associations were in sandy soil, and their vegetation has been described in detail by GLEASON.[4] A brief description of the vegetation and the successional relations of the associations, however, may be given here.

The standard.—During standardization the atmometers were placed on the ground in the Chautauqua Park athletic field, and the standard instrument was kept there during the whole period of observation. This field was formed by leveling the sandy ground after cutting off the mixed forest association which covered it. It was bordered by a cultivated field on the east, and was surrounded on the other three sides by forest at a distance of 50–100 m. from the atmometers. The field was partly covered by weeds, of which the following were the most abundant: *Erigeron canadensis*, *Mollugo verticillata*, *Eragrostis Purshii*, *Erigeron divaricatus*, *Verbena stricta*, *Erigeron annuus*, *Cenchrus carolinianus*, and a few other grasses. The atmometers were placed in the center of an area cleared of the taller weeds for a radius of about one meter (fig. 1).

The river bank.—One atmometer was maintained on the sandy eastern bank of Quiver Lake, at a height which corresponds to a

[4] GLEASON, H. A., The vegetation of the inland sand deposits of Illinois. Bull. Ill. State Lab. Nat. Hist. **9**:23–174. *figs. 6. pls. 20.* 1910.

reading of 15 feet above the zero of the Havana gauge, located about 2.5 km. south. The lake has a continuous connection with the Illinois River, forming an expanse of water about 400 m. wide. During the course of the experiment the river fell from 12 to 7.8 feet on the Havana gauge. The location of the atmometer was selected to show the evaporation from an open surface near the

FIG. 1.—Atmometers in process of standardization, June 22, 1910; photograph by F. C. GATES.

water. The ground is sandy and for the most part without vegetation because of its regular inundation during high water in the river. The plants that occur along the beach are mostly sand plants, such as *Sporobolus cryptandrus*, *Cenchrus carolinianus*, and *Opuntia Rafinesquii*. There are some relics from the mixed forest above, as *Clematis Pitcheri*, and numerous xerophytic weeds, as *Melilotus alba*. A few trees still grow at the water's edge, but most of the original shore vegetation has succumbed to the effect of the higher average level of the water since the opening of the Chicago

Drainage Canal. The evaporation from this atmometer was very pronounced during the day, but was much lower at night. Sometimes virtually no nocturnal evaporation was indicated, while on the athletic field, about 200 m. inland and separated from the river by a forested dune, the evaporation was quite noticeable.

The bottom-lands.—The bottom-lands immediately across the river show plainly the results of the persistent high water during the last few years. The low banks and islands between the numerous lakes are still mostly covered with trees, but they are gradually being killed. A marginal zone of *Salix longifolia* represents the *Salix-Cephalanthus* association, while in the interior or highest parts of the islands a few maples, *Acer saccharinum*, occur, showing the former presence of the *Ulmus-Acer* association. A few pecan trees, *Carya illinoensis*, are present, but other tree species are rare. The ground is submerged during the greater part of the year. If emergence occurs during the summer, the surface is in a few weeks thickly covered with a growth of weeds, of which the most abundant are *Xanthium commune*, species of *Aster*, and other composites, and with numerous seedlings of willow and maple, none of which, however, survives the following winter. One atmometer was placed in a large rotten willow stump, about 6 m. from the river bank and about 2 m. above the surface of the mud. When first located, the station was covered half a meter deep with water. Another instrument was stationed in a maple stump, 1.7 m. above the mud, and about 8 m. from the river (fig. 2). Since the maple leaves were more nearly confined to the upper parts of the trees, while the willows were leafy almost to the ground, the better circulation of air permitted a greater evaporation under the maple trees.

The bunch-grass association.—Of the several consocies of the bunch-grass association occurring in the region, two adjacent ones were selected, characterized respectively by *Eragrostis trichodes* and *Leptoloma cognatum*. The former of these is the more stable, and consists chiefly of well defined bunches of *Eragrostis* spaced about 2–4 dm. apart. Other less conspicuous or less abundant grasses occur also, particularly *Andropogon furcatus*, *Leptoloma cognatum*, *Sorghastrum nutans*, and *Paspalum setaceum*, with a few plants of

other species. Scattered among the grasses are plants of several secondary species which fill the spaces between the bunches and give the area the appearance of a closed association. The more prominent of these are *Lespedeza capitata*, *Opuntia Rafinesquii*, *Crotonopsis linearis*, *Ambrosia psilostachya*, *Oenothera rhombipetala*, *Lepidium virginicum*, *Krigia caroliniana*, *Cyperus Schweinitzii*,

FIG. 2.—The center of a willow island, showing atmometer no. 1 on a maple stump, July 9, 1910; photograph by F. C. GATES.

Specularia perfoliata, *Croton glandulosus*, *Erigeron canadensis*, *Commelina virginica*, *Monarda punctata*, *Callirhoe triangulata*, *Carex Muhlenbergii*, and *Erigeron strigosus*.

The *Leptoloma* consocies, which is very abundantly represented in this region, is a less stable type of bunch-grass. The dominant species, *Leptoloma cognatum*, does not form bunches as well defined as those of *Eragrostis trichodes*, but with its spreading habit and irregular bunches occupies a larger proportion of the area. With it are associated a few other grasses, especially *Panicum pseudo-*

pubescens, *Cenchrus carolinianus*, *Sporobolus cryptandrus*, and *Bouteloua hirsuta*, with less of *Paspalum setaceum* and *Andropogon scoparius*. The secondary species are not numerous, but a few species are so conspicuous at certain seasons of the year that they make distinct aspects. The *Oenothera rhombipetala* aspect dominated during the period in which this experiment was conducted. The most important secondary species are *Opuntia Rafinesquii*, *Lepidium virginicum*, *Ambrosia psilostachya*, *Tephrosia virginiana*, *Chrysopsis villosa*, *Monarda punctata*, *Croton glandulosus*, *Oenothera rhombipetala*, *Cyperus Schweinitzii*, *Tradescantia reflexa*, *Specularia perfoliata*, *Lithospermum Gmelini*, *Petalostemum purpureum*, *Draba caroliniana*, *Euphorbia Geyeri*, *Lespedeza capitata*, *Krigia caroliniana*, *Cassia Chamaecrista*, *Pentstemon hirsutus*, *Antennaria* sp., and *Aster sericeus*. The atmometers in these two consocies were about 15 m. apart.

The blowouts.—The blowouts are excavations in the mobile sand caused by the action of wind. In this region nearly all of them are surrounded by the bunch-grass prairie. The sand is virtually free from vegetation except for a few species, such as *Acerates viridiflora*, var. *lanceolata*, *Cristatella Jamesii*, and *Aristida tuberculosa*, which find here their preferred habitat. The dry surface layers of the sand are blown by every wind, and become very hot on sunny days. One atmometer was placed in the bottom of the complex known as the Devil's Hole, 3 km. east of Havana, and another half-way up its lee slope toward the east (fig. 3).

The Quercus velutina association.—The first forest association to appear on the sand in this region is characterized by *Quercus velutina* and *Q. marilandica*. Of the two, the former is usually more abundant and better developed. In typical situations other species of trees are seldom present. In general, *Q. marilandica* tends to occupy the poorer soil, and is more frequently the first to appear on cleared or lumbered land, but *Q. velutina* seems to be more persistent and better able to hold its own. The presence of trees of *Carya cordiformis* may indicate an incipient succession of the mixed forest association. Actual count of the trees in the vicinity of one atmometer showed that 57 per cent of the old trees were *Q. velutina*, 42 per cent *Q. marilandica*, and 1 per cent *Carya*

cordiformis. In the typical areas of this association, there are neither vines nor shrubs, with the exception of some shrubs remaining as relics from the prairie, even though the seeds are already present in the sand beneath the trees. The presence of *Psedera quinquefolia* and other vines in some places is accordingly considered an indication of the approaching succession of the mixed forest

FIG. 3.—A blowout near the station of atmometer no. 8, July 1910; photograph by ARTHUR G. VESTAL.

association. The shrubby growth consists largely of the young trees of the dominant species, together with *Rhus canadensis*, var. *illinoensis*, and *Ceanothus americanus*, relics from the bunch-grass. The herbaceous vegetation but sparsely covers the ground, although the number of species represented is usually large. The most common and typical are *Tradescantia reflexa*, *Amorpha canescens*, *Euphorbia corollata*, *Smilacina stellata*, *Phlox bifida*, *Verbascum Thapsus*, *Monarda fistulosa*, *Lithospermum Gmelini*, *Aster azureus*, *Rudbeckia hirta*, *Lespedeza capitata*, *Pentstemon hirsutus*, *Asclepias tuberosa*, *Tephrosia virginiana*, and *Rosa humilis*. The soil is sand

to within a few centimeters of the surface, which is covered with a layer of dead but undecayed leaves. Two atmometers were maintained in woods of this type about 500 m. from the bunchgrass and blowouts. One of them was in a typical area of the vegetation (fig. 4), and the other in an area in which there were numerous young trees of *Carya cordiformis*.

FIG. 4.—Interior of *Quercus velutina* association, showing atmometer no. 7, July 9, 1910; photograph by F. C. GATES.

The mixed forest association.—In the mixed forest more than half of the trees are of species typical of the *Quercus velutina* association which has preceded it. In this particular area, the oldest trees are without exception *Quercus velutina*, while near the edge there are some large *Q. marilandica*. There are also numerous young trees of *Carya cordiformis*, which are nearly as large as the more slowly growing oaks. Scattered among the individuals of these three species are a few trees of *Gymnocladus dioica* and *Celtis occidentalis*, the latter only near the margin. An actual count of

the trees near the atmometer gave the following results: *Carya cordiformis*, 62.5 per cent; *Quercus marilandica*, 19.2 per cent; *Q. velutina*, 14.3 per cent; *Celtis occidentalis*, *Gymnocladus dioica*, and *Quercus rubra*, each 1 per cent. The proportion of the young trees, however, is very different. Between 80 and 90 per cent of them are *Carya cordiformis*. They dominate in every clearing, although occasionally they are accompanied by a few young trees of *Quercus velutina*. Young trees of *Q. marilandica* are not at all plentiful and occur only at the edges. The luxuriance of the growth of vines is the most prominent feature of the change from the *Quercus velutina* association. Nearly everywhere in the mixed forest vines are the conspicuous ground cover. This is never true of the typical *Quercus velutina* association. Most prominent of these is *Psedera quinquefolia*, which not only carpets the ground with green, but also climbs to a considerable height. More noticeable as climbers, however, are *Celastrus scandens* and *Vitis vulpina*. Shrubs are prominent only near the margin of the association, although a few species are scattered throughout. The commoner species of the herbaceous vegetation are *Scrophularia leporella*, *Anychia canadensis*, *Parietaria pennsylvanica*, *Hedeoma pulegioides*, *Asclepias phytolaccoides*, *Galium circaezans*, *Aquilegia canadensis*, *Galium pilosum*, *Silene stellata*, and *Cacalia atriplicifolia*. Two atmometers were maintained in this association. One was located near the margin of the grove, while the other (fig. 5) was near the center.

From an inspection of the data given in the diagram it is seen that the bunch-grass, the blowout, the *Quercus velutina*, and the mixed forest associations all show noticeably different amounts of evaporation. The instruments in these associations were located within half a kilometer of each other, in a region of comparatively uniform topography. The variation in the physical factors of the environment is not sufficient to explain the wide variation in the amount of evaporation. Accordingly the vegetation, which is the most variable factor of the environment, appears to be the essential factor in determining the evaporation rate. This, however, is accomplished indirectly, since vegetation influences evaporation chiefly through the control or modification of the wind, the temperature, and the humidity, all of which affect the evaporation

directly. The diagram shows also that those associations which stand high genetically have a lower evaporation rate than those genetically lower in the successional series.

This relation between succession and evaporation is best shown in the sand dune habitats, where four sets of atmometers were maintained. The original vegetation there is the bunch-grass

FIG. 5.—Interior of the mixed forest association, showing atmometer no. 11, July 9, 1910; photograph by F. C. GATES.

association, but under certain conditions portions of the association may be destroyed by wind action, resulting in open areas of bare sand, the blowouts. The present blowouts are all of secondary origin, but their environment and vegetation probably represent the primitive condition of the region, shortly after its emergence from the glacial Illinois River. In these blowouts the highest evaporation occurs. The blowout is eventually revegetated by bunch-grass, during which process two or more consocies of the bunch-grass association appear. The *Leptoloma cognatum* consocies

is usually the earliest one to develop, and later is followed by the *Eragrostis trichodes* consocies. The latter, representing the higher development of the association, has an evaporation rate which is 88 per cent of the lower type. In both cases the amount of evaporation from the bunch-grass is lower than that from the blowout, although the four atmometers were less than 100 m. apart.

The difference in the rate of evaporation in the bunch-grass and *Quercus velutina* associations is much more marked. Young oak trees in different stages of development are present in the former

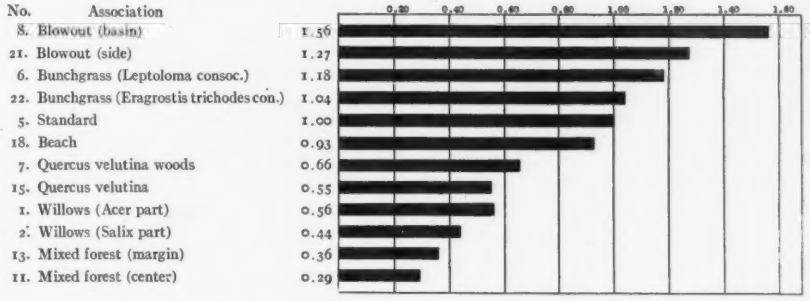
No. Association
8. Blowout (basin) 1.56
21. Blowout (side) 1.27
6. Bunchgrass (Leptoloma consoc.) 1.18
22. Bunchgrass (Eragrostis trichodes con.) 1.04
5. Standard 1.00
18. Beach 0.93
7. Quercus velutina woods 0.66
15. Quercus velutina 0.55
1. Willows (Acer part) 0.56
2. Willows (Salix part) 0.44
13. Mixed forest (margin) 0.36
11. Mixed forest (center) 0.29

FIG. 6.—Diagram showing relative amounts of evaporation in the different stations.

association, clearly demonstrating that they are capable of withstanding the relatively high prairie rate of evaporation. With their growth to maturity, and the consequent succession of the bunch-grass by the forest, the evaporation beneath them is steadily diminished, until it becomes about 55 per cent of that of the normal bunch-grass. Atmometer no. 7 was placed in a typical part of the *Quercus velutina* association (fig. 4).

With the increase in the age and density of the forest cover, the evaporation beneath it is still further reduced. Eventually the succession of the mixed forest association begins, and the first indication is usually shown by the presence of *Psedera quinquefolia* and *Celastrus scandens*. Atmometer no. 15 was located in such a place, and the diagram shows a reduction in the rate of evaporation from 0.66 to 0.55, in terms of the standard. The reduction is still greater in the typical mixed forest, represented by instruments

11 and 13, the latter of which was placed near the border of the association, while the former was in the center. With the establishment of the mixed forest association the sand area reaches the present culmination of the successional series. Throughout this series the amount of evaporation has steadily decreased, reaching its lowest rate in the association genetically highest.

Actual observation shows that the succession of the bunch-grass by the *Quercus velutina* association begins in the normal association, where the rate of evaporation is high. It also shows that members of the mixed forest association appear in the *Quercus velutina* association while the evaporation rate there is still relatively high. In both cases the development of the association reduces the evaporation. Succession, therefore, does not depend upon evaporation; it is a cause rather than an effect.

The other records shown in the diagram are not to be placed in this genetic series. Sufficient instruments were not at hand, nor does this particular locality give the opportunity for investigation in the series of associations beginning with the open water and ending with bottom-land forests. Nevertheless, one or two points are brought out, notably that the evaporation on the open sand of the river beach is not nearly so great as that from the open sand of a blowout. The river is here a most important factor, tending to reduce the extremes of temperature during the day, and maintaining a relatively high humidity during the night. Evaporation from the willow and maple islands was greater than from the mixed forest, although the latter grew in dry upland sand, and the former in mud, during part of the experiment covered and at all times surrounded by large bodies of water. This is simply another instance indicating that the vegetation is of greater importance than the physical environment in controlling evaporation.

Conclusions and summary

1. Since proper conditions for maintaining an absolute standard were lacking, the results were all calculated on the basis of one instrument arbitrarily chosen as a standard, and are represented in relative terms only.

2. Differences in the amount of evaporation in various associations are due chiefly to the nature of the vegetation, which by its size and density controls the evaporation beneath it.

3. The observations indicate that successions between associations are not caused by any conditions of evaporation.

4. The more primitive associations have the higher rates of evaporation, while those most nearly like the climax type have the lowest rates. This is true not only for the forest associations, in which low evaporation is expected, but also for the prairie associations, which are correlated with an arid climate and consequently high climatic evaporation.

The standardization and field observation of the atmometers and the evaluation of the relative rates of evaporation were managed entirely by the junior author; for all other statements both authors are responsible.

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A STUDY OF TARGIONIA HYPOPHYLLA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 156

HERMANN DEUTSCH

(WITH THIRTEEN FIGURES)

Considerable work has already been done on the morphology of *Targionia hypophylla*, LEITGEB (1) and CAMPBELL (2) being foremost among the investigators. Recently CAVERS (3) also published a paper on the same species; but with all this there still remains some little ground which has not been covered at all, as well as some which has been covered but superficially. These points it is the aim of this paper to try to clear up.

The material for this study was collected in 1908 by Drs. BARNES and LAND along the steep slopes of the canyon of the Rio Santiago in western Mexico, and also on the eastern slope of Mt. Orizaba. In both regions it was found only at an altitude of 1500 meters.

Gametophyte body

The thallus in this group is about as complex as in any of the Marchantiales. This statement is not based on any one of the several characters that usually distinguish a thallus as simple or complex, but on an average of the total amount of differentiation and complexity present.

In the first place, the thallus is formed by the segmentation of a single, cuneate apical cell (figs. 1 and 2), cutting off segments on four faces. CAVERS (3) reports a row of initials at the apex. In none of the preparations studied in this particular instance, however, could this report be verified. On the contrary, they seemed to show very distinctly a single apical cell, distinguished from its surrounding segments both as to its size, and also as to the size, plane, and position of its nucleus. Relative to the apical cells found in the other genera of the Marchantiales, the apical cell of *Targionia* is rather small.

The development of the air chamber is one feature which, as yet, has not been described. This proceeds along the lines reported by

BARNES and LAND (4) as typical for the Marchantiales. The air chambers arise by the splitting apart of the superficial cells just

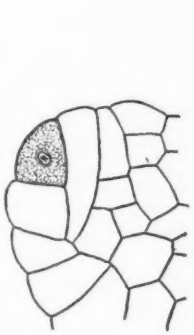

FIG. 1

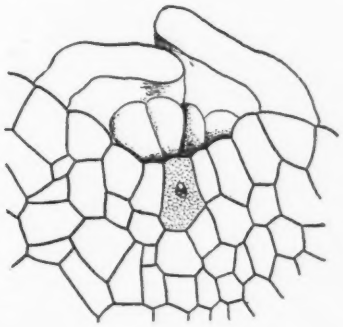

FIG. 2

FIGS. 1, 2.—Fig. 1, median longitudinal section through the apical cell; fig. 2, section in horizontal plane of thallus through the apical cell.

back of the growing point (fig. 3). However, in the other Marchantiales described, this splitting originates in an angle between the epidermal and hypodermal layers of cells, and proceeds outward toward the surface; in *Targionia* the process is reversed, the cracking apart starting at the surface between two epidermal cells and proceeding inward. Subsequent divisions enlarge the space thus formed, as well as the breadth of the roof.

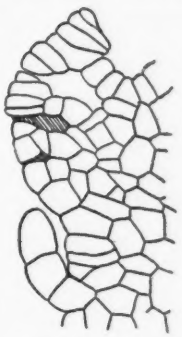

FIG. 3.—Nearly median section through growing point, showing origin of air chambers.

Early in its development the pore is closed by rapid divisions in the roof cells, and it remains closed until the chamber has almost reached maturity. The chlorophyllose filaments develop comparatively early in the history of the chamber (figs. 4–6); as soon as the chamber is 3–5 cells broad, the cells of the floor begin to project as papillae. These papillae are divided by transverse walls into filaments, which at maturity are 2–6 cells in length. They branch profusely, and in the mature chamber very

often are so long that they grow snugly up against the roof, thus giving the impression, in section, as though there were filaments depending from the roof of the chamber, as well as standing up from the floor. Directly beneath the pore the filaments are slightly modified, the distal cell being hyaline and containing no chloroplasts except one or two lying along the bottom wall. There is no modification in the form of

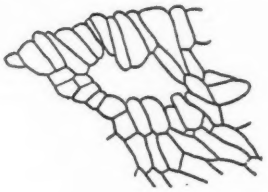

FIG. 4

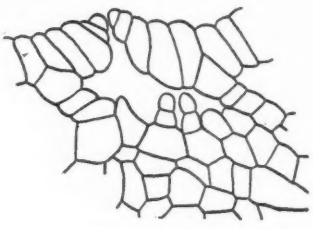

FIG. 5

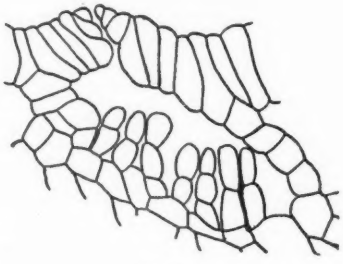

FIG. 6

FIGS. 4–6.—Fig. 4, young air chamber before appearance of the chlorophyllose filaments; fig. 5, air chamber with two chlorophyllose filaments and primordium of a third; fig. 6, later stage of air chamber, showing distortion due to unequal elongation of cells of the thallus.

these hyaline cells, as there is in *Conocephalus;* they retain the same ovoid shape found in the other cells of the filament (figs. 7 and 8).

The cells surrounding the air pore are arranged in a series of concentric rings, raised crater-like a little above the dorsal surface of the thallus. The innermost ring is composed of dead cells, collapsed and highly cutinized; and is not, as stated by CAVERS, a hardened membranous ring which has been put forth by the innermost layer of cells surrounding the pore (fig. 9).

The ventral scales are placed in two rows on either side of the midrib and are of an intense dark purple or red-brown color. They are inserted on the posterior margin, and arranged on the ventral surface in a wonderfully exact and regular fashion. On the anterior margin of the scale is borne a curious little appendage (fig. 10)

which in the younger scales overlaps the growing point of the thallus, and may serve as a protective covering. The two rows of

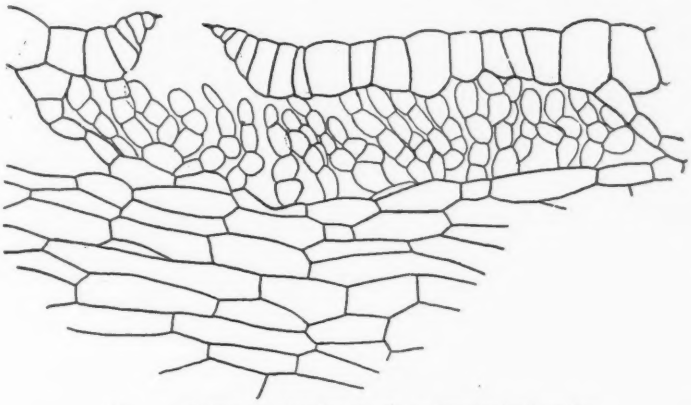

FIG. 7.—Mature air chamber in median longitudinal section

scales are separate from the first, arising from young segments close to the apical cell (CAMPBELL 2).

Both the pegged and the smooth rhizoids are present. They are extremely long, and most curiously swollen and distorted at the distal end. According to CAVERS (3) the smooth rhizoids are borne on the midrib and pass directly into the ground. The pegged rhizoids arise in great profusion in the axils of the scales and pass backward along either side of the midrib.

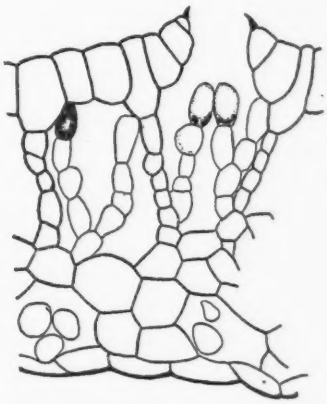

FIG. 8.—Transverse section through two air chambers, showing their extreme narrowness.

The solid, colorless tissue of the thallus is composed of elongated and, for the most part, highly vacuolate cells. These begin their elongation directly behind the growing point, and this process goes on so rapidly

that it pulls both the filaments and the vertical walls of the air chambers diagonally backward, giving the chamber a more or less distorted appearance (figs. 4–7).

A really surprising amount of differentiation is seen in the cells of the solid portion of the thallus. The commonest and most usual is a strand of stumpy cells, filled with oil globules and food granules, which passes longitudinally through the center of the thallus, and ends around the foot of the sporophyte. Besides this, there is frequently a strand composed of the ordinary elongated cells, with their walls thickened by an irregularly wound tangle of fibers, also running the entire length of the thallus.

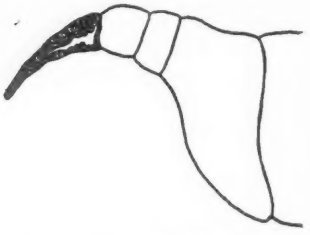

FIG. 9.—One member of the ring of collapsed cells which surround the air pore.

Vegetative reproduction.—The dichotomous branching, which is so common in the other members of the Marchantiales, is here almost entirely replaced by the occurrence of branches arising from the ventral surface. These branches have, for the most part, at maturity a stalk-like base, through the dying away of which the branches are set free as independent plants, and will then themselves multiply in the same fashion.

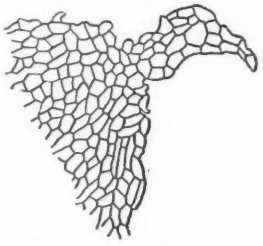

FIG. 10.—Appendage to ventral scale, which overlaps the growing point.

In their origin, these adventitious branches have absolutely nothing to do with the apical cell. This was clearly seen in several of the preparations studied, where, on a plant bearing two young branches, the older one was placed between the apical cell and the younger.

Archegonia.—The archegonia are borne terminal on the thallus. They follow so closely the general line of individual development for the Marchantiales, that it is not necessary to repeat it here. They arise in two rows in acropetal succession. The surface, or pad, on

which they are borne slopes forward and downward at the time the archegonia are mature. The development of this "fruiting surface" runs as follows. The archegonia, arising as they do in acropetal succession, check to a great extent the vegetative growth behind the growing point. The apical cell, however, is not immediately concerned, and continues its segmentation with practically no interruption. The natural result of this is that the apical cell is carried forward and out. Thus the archegonial surface is finally brought to lie in a sort of pit or depression in the anterior end of the thallus. On the lower and outer margin of this pit is the apical cell, which, when this stage is reached, ceases to function.

The involucre.—The development of the involucre is so closely allied to that of the archegonial surface, that it is extremely difficult to say just where the one leaves off and the other begins. It is simply the continued forward growth of the tissues immediately surrounding the shallow pit at the anterior end of the thallus, with the natural result that the opening to this pit is narrowed, and begins to close up. It is never completely closed, however, although in the earlier stages the edges of the wings are brought very close together. As the involucre matures, the outer surface, as well as the inner margin of the wings, becomes highly cutinized.

That the involucre is not, as reported by CAVERS (3), a result of the stimulus given by the act of fertilization is shown in one of the preparations, where it was complete and well developed, while the eggs of the archegonia it surrounded were still unfertilized.

Calyptra.—The calyptra is a simple and very delicate structure, soon ruptured by the growth of the sporophyte. At maturity it is 2–4 layers thick at the base.

Sporophyte body

Capsule.—The capsule is a comparatively simple affair. The wall consists of a single layer of cells, uniformly thickened with spiral and annular bands. There is no special mechanism for dehiscence. In his recent report on *Targionia*, CAVERS (3) figures and describes a rudimentary elaterophore, represented by a few spirally thickened cells depending from the distal portion of the capsule. This statement could not be verified in any of the sections

studied here, nor do either CAMPBELL (2) or LEITGEB (1) report such a condition.

True elaters are present, long, slender, fusiform, and thickened by usually two spiral bands.

The spores themselves have fairly thick walls, highly sculptured, and are produced in great numbers (fig. 11). CAVERS (3) has described the spore mother cells as lobing deeply before division, as happens in many of the Jungermanniales. All of the preparations studied here, however, show the ordinary tetrad formed from a spherical spore mother cell.

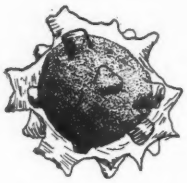

FIG. 11.—Tuberculate spore.

Seta and foot.—Both seta and foot are rather well developed. While small as compared with the size of the capsule, they are nevertheless rather massive, and well differentiated from each other. The foot is club-shaped, and bluntly pointed at the lower end (fig. 12). The surface cells project as short papillae, and are haustorial in function. These cells, as well as those of the calyptra surrounding them, show in section a very much darker stain than do the cells of the surrounding tissues. Between the calyptra and foot is interposed a fairly thick layer of mucilaginous material.

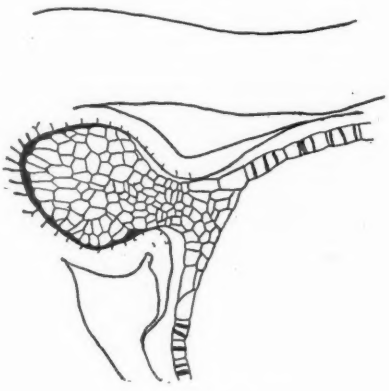

FIG. 12.—Foot and seta

Although 6–10 archegonia are produced, only one egg is fertilized. The remaining archegonia, however, persist, and are still visible after the sporophyte has matured; soon after the sporophyte has begun its development, however, their contents break down into a darkly staining mucilaginous mass.

Classification

The Marchantiaceae are at present classified according to three schemes. LEITGEB (**1**) gives the following:

Marchantiaceae
- *a*) Astroporae (Clevea, etc.)
- *b*) Operculatae (Plagiochasma, Fimbriaria, etc.)
- *c*) Targioniae (Targionia, Cyathodium)
- *d*) Compositae (Marchantia, Lunularia, etc.)

CAMPBELL (**2**, p. 67) gives the following:

Marchantieae
- *a*) Corsinieae
- *b*) Targionieae
- *c*) Marchantieae

GOEBEL has proposed still another classification. In this he transposes the Riellaceae to the *Marchantia* group, as follows:

- *a*) Corsiniaceae
- *b*) Targioniaceae
- *c*) Riellaceae
- *d*) Marchantiaceae

Without concerning ourselves with the relative merits of these schemes, it might be well to take up the one family, the Targionieae. This family at present contains but two genera, *Targionia* and *Cyathodium*, and it is with regard to the merits of placing these two genera within the same family that a question may be raised. In order the more clearly to present this question, the accompanying diagrams (fig. 13) have been prepared. In the key to these diagrams it will be seen that each generation (sporophyte and gametophyte) has been divided into four features, selected because of their bearing on a natural scheme of classification. Each of these divisions has been subdivided into five stages of as nearly equal importance as it was possible to find.

From the diagram it will be seen that the two lines coincide in but two points. The one of these is D_4 and the other E_4, which represent respectively the apical position of the archegonia accompanied by a checking of the growth of the thallus at this point, and the common involucre.

As for the former (D_4), the character is not peculiar to this

group. In several other genera the archegonia are borne in a terminal cluster, notably *Grimaldia*, *Reboulia*, and *Clevea*. This narrows the situation down to a *single* character common to these two genera (*Targionia* and *Cyathodium*) and not found in others. This is the common involucre inclosing the terminal group of archegonia.

One glance at the diagrams will show how widely the two genera differ in all other respects save this. *Targionia* has perhaps as complex a thallus as is found in the entire group of Marchantiales;

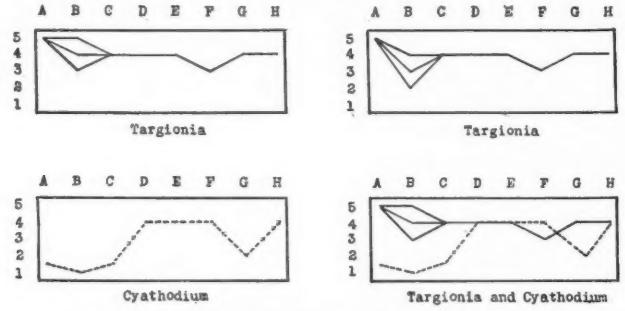

FIG. 13.—Diagrams comparing *Targionia* and *Cyathodium*

Cyathodium has perhaps the simplest, both as regards structure and the amount and character of differentiation. The thallus of *Cyathodium* consists of a simple ribbon, two layers of cells thick, the two layers slightly separated to form an air space, the air pores being simple openings in the upper layer of cells.

In *Targionia* the antheridia are borne on a special portion of a special branch; in *Cyathodium* they are scattered in clusters along the edge of the thallus. In *Targionia* the foot and seta of the sporophyte are massive and well differentiated; in *Cyathodium* both foot and seta are represented by a single filament, four cells in length.

In *Targionia* the elaters are true elaters, long pointed, and spirally banded; in *Cyathodium* the elaters, while spirally banded, are little more than dead nurse cells, short and stumpy.

In but one character is *Targionia* less advanced than *Cyathodium*, and that is in the differentiation of the capsule wall

KEY TO DIAGRAM FIG. 13

	Gametophyte body				Sporophyte body			
	Air chamber	Solid nutritive region	Antheridia	Archegonia	Protection	Capsule	Foot and seta	Sporogenous tissue
	A	B*	C	D	E	F	G	H
1....	Clefts	undiff. solid tissue	scattered	on pad	thallus over-growth	single layered	none	all forms spores
2....	Riccia type	differen. central strand of soft tissue	intermittent formation (groups)	stalked pad	antheridial pad	irregularly thickened	filament	some of the cells die and lose contents
3....	Plagiochasma type	same with central cells thickened and dead	pad or cushion	arch. at apex without interfering with growth	thallusfold	uniformly spirally thickened	quadrant-octant	these cells thickened
4....	Marchantia type	both above combined	terminal pad	apical growth checked	common involucre	thickened along lines of dehiscence	massive and comparatively small	elaters present
5....	Conocephalus type	radio-dorsi-ventral	compound receptacle	compound receptacle	separate involucre	multi-layered at top or bottom	massive and large	elaterophore present

* In case we do not accept GOEBEL's inclusion of the Riellaceae, the fifth character here given is omitted, the other four each moved up one step; while, as the lowest character, we split off from the second one here those thalli having only two layers, which are separated slightly, the space between forming an air chamber, so that the solid nutritive portion of the thallus consists of but a single layer of cells.

in the mature sporophyte. In *Cyathodium*, only the cells of the upper part of the capsule are spirally thickened, so that dehiscence occurs through the formation of 6–8 fairly regular teeth.

Of course there are several difficulties in the way of such a determining scheme as this. In the first place, it is next to impossible to select characters that will be absolutely determining. In the second place, it is impossible to select groups of characters whose determining value will be equal. Again, there is the difficulty of deciding as to which of two characters is the more advanced. And finally, there is the conflict as to the relative value of sporophytic and gametophytic characters. Is a complex gametophyte with a simple sporophyte more advanced than a simple gametophyte bearing a complex sporophyte, or vice versa; to say nothing of the different gradations in combining the two.

Leaving aside, for the present, the difficulties which a practical application of this scheme presents in general, it does seem to apply in the specific case under discussion; no matter which of the two is the higher, it seems to be fairly certain that they are widely different. According to the diagrams the two genera have but the one salient feature which is common to them and to them only, a single involucre inclosing a group of terminally borne archegonia. Now it certainly does not seem as though such a character as this should be sufficient to bind two genera differing so widely in all other respects into one family.

As to where *Cyathodium* belongs, if not with the Targionieae, the Corsinieae suggest themselves readily. But such a matter as this cannot be settled definitely without a much more extended study of *Cyathodium*, as well as the family Corsinieae, with its two genera (*Corsinia* and *Funicularia*), than has been given them.

Thanks are due Professor JOHN M. COULTER and Dr. W. J. G. LAND for assistance rendered during the progress of the work.

THE UNIVERSITY OF CHICAGO

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A PRECISION AUXANOMETER

W. T. Bovie

(WITH TWO FIGURES)

In the auxanometers which have been described up to the present time, a thread or string has been used to transmit the motion of the growing plant to the recording device. This construction is always faulty, because changes in humidity affect the length of the thread, and so falsify the record. The author has designed a machine which eliminates the thread and its unavoidable errors by substituting for it material which is not affected by humidity and which is very little altered by changes in temperature.

On account of the error due to the thread, it has heretofore been impracticable to use a recording device which would indicate small increments in length. On account of the great precision of the new instrument such a device is needed, and accordingly the recording mechanism has been refined until it is capable of registering an increment of a single micron.

It has hitherto been necessary, except with the auxanometer described by FROST,[1] to place the recording device in close proximity to the plant. This is cumbersome and has prevented the simultaneous recording of the growth of a number of plants. FROST'S machine used a thread, but as the growth was recorded electrically, simultaneous records of the growth of several plants could be made. This valuable feature has been incorporated in the new auxanometer.

The machine consists essentially of a device which is carried upward as the plant grows. When this device has moved a certain small distance, it closes an electric circuit which operates the recording pen of a chronograph. As the connection of the plant with the circuit-closing device is made with invar, a metal with an exceedingly small coefficient of expansion with changes of temperature, the growth can be accurately measured to a very few microns, and by using a condenser in the electric circuit, as described later, the growth can be recorded to a single micron.

[1] Minnesota Botanical Studies no. 17. 1894.

The mechanism may be understood by referring to fig. 1. The plant is attached by the invar wire *a* to the small spring *b*, which pulls upward a little more than is necessary to lift the weight of the wire (the exact amount of this pull may be regulated easily by a screw not shown in the drawing). Experiment has shown that this slight pull is not enough to affect the growth of the plant.

As the spring moves upward, it comes in contact with the block *c* at the point *c'*. This closes the electric circuit, which up to this time has been open, since the spring *b* is insulated from *c* at its other point of contact. The current which now flows through the line energizes the coil *d*, which draws the escapement lever upward. The block *c* is carried on the screw *f*, which is connected by a train of wheels at *f'* to a clock spring, which tends to turn the screw in such a manner as to raise the block *c* upward. The screw is prevented from turning by the escapement lever *e*, but when the escapement lever is drawn up by the magnet *d*, it allows the screw to turn a given part of a revolution. The block *c* is therefore raised a certain distance and the circuit opened. The plant must now grow exactly this distance before the circuit is closed again.

The upward movement of the block *c* is determined by the pitch of the thread of the screw *f* and the amount it turns. By changing the number of teeth in the escapement wheel at the top of the screw *f*, the amount it turns at each contact can be controlled. There are 20 teeth in the escapement wheel, and so the screw can be made to turn 1/20 of a revolution, or if part of the teeth are removed, it will turn more, up to a complete revolution. If the pitch of the screw is 0.5 mm., each record represents 25μ.

It may be noted, in passing, that the micrometer screw has become the standard device for measuring small distances. It is not the purpose of this account to give the mechanical specifications of the apparatus; there are many ways in which the various details can be constructed. It may be said, however, that the screw should be straight and accurate. (The screw from a phonograph, with its nut, is an excellent and inexpensive micrometer.) It should turn easily and run true in its bearings, and the nut in the block *c* should be so constructed as not to bind. In this machine use is made of a split nut which is tightened by a conical cap into which it fits.

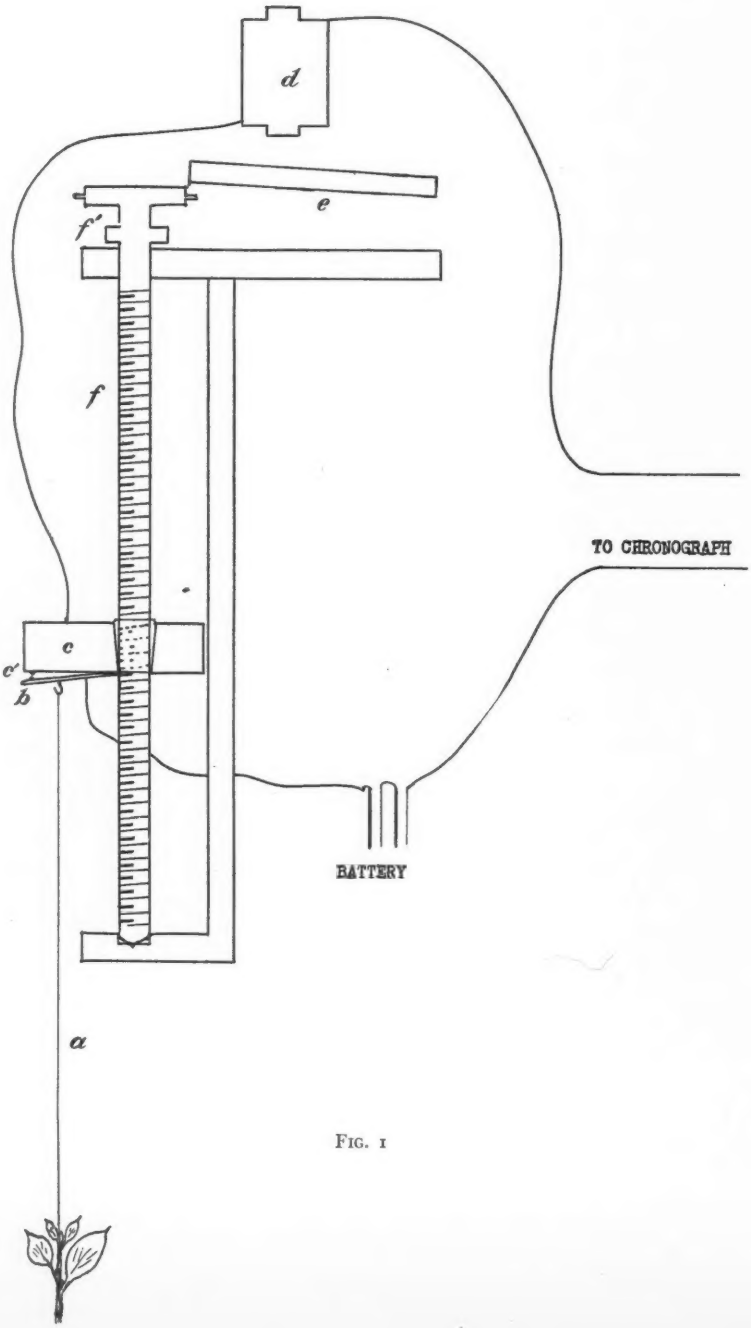

FIG. 1

The escapement should be such that one (and only one) tooth of the escapement wheel can pass at one closing of the circuit. This becomes important when the screw has to make a complete revolution for each record.

The chronograph was constructed especially for this apparatus. The drum turns once in six hours, and is of such a diameter that 1 mm. on the drum corresponds to one minute in time. The drum is long enough to receive the records from six auxanometers at one time, and holds one week's record. The pens are stationary, the drum turning under them and moving forward in the line of its own axis, so that each pen traces a spiral on the record sheet. At each closing of the circuit the pen makes a check in the line traced. When the record is removed for reading, we have a series of parallel lines, each representing six hours of time. By counting the number of checks in a given length of time, or by measuring the distance between the checks, the rate of growth can be determined.

By means of a small switchboard, an electric bell or an electric light can be included in the circuit, so that each time an increment of growth is recorded the light flashes and the bell rings. This is used only for lecture experiments. A tungsten lamp should be employed, as the length of contact is so short that an Edison lamp does not have time to become luminous.

An elongating hyacinth peduncle, which had been in the damp greenhouse and was removed to the dry air of the lecture-room, gave a record a little oftener than once a minute. Had the plant been left in the greenhouse and only the chronograph taken to the lecture-room, the contacts would have been more frequent. A young sunflower seedling gave a record every 18 seconds. Such records are too frequent for experiments of long duration, as there are too many checks to count. When working with plants growing at this rate, some of the teeth in the escapement wheel should be removed.

The principle of having the plant automatically close and open an electric circuit during growth permits the increase in length to be measured to almost any degree of accuracy. The only difficulty is a tendency to arcing across the spark gap between the spring *b* and the block *c*. There are two ways of preventing this: the wire

a may be attached near the fixed end of the spring *b*, thus making the gap longer than the distance recorded, or a condenser (such as is used in a telephone for instance) may be placed around the gap. The latter method will also tend to prevent burning of the terminals. Terminals of platinum and gold give the best results. Even with these precautions there will be a limit to the accuracy of a

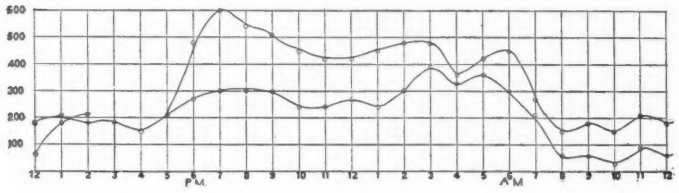

FIG. 2.—Curve of rate of growth of the hypocotyl of a four-o'clock seedling; abscissas indicate time, ordinates growth per hour in microns; total time recorded, 46 hours; total growth recorded, 1.75 cm.

Time	1	2	3	4	5	6	7	8	9	10	11	12
Checks per hour	..	..	..	5	7	16	20	18	17	15	14	14
	15	16	16	12	14	15	9	5	6	5	7	6
	7	6	6	5	7	9	10	10	10	8	8	9
	8	10	13	11	12	10	7	2	2	1	3	2
	6	7	..	..	..	..	..	..	..	..	..	..

single record, for the two metal surfaces will not always give electrical contact at the same place. But as any experiment includes a great number of records, these slight errors will average up so that the results will be absolutely accurate.

A record is given in fig. 2 of a four-o'clock seedling for the first 46 hours after it appeared above the ground. The making of this record put the machine to an extreme test, as these seedlings are very delicate. It will be noted that the curve is very even, and that it passes very close to the points from which it is plotted. The relation of the rate of growth to light is clearly shown. The records were made in January, when the laboratory darkened early. The temperature of the laboratory falls considerably at night, getting coldest at 4 o'clock in the morning, at which time the day fireman starts up the fires. It will be noted that on both nights the rate of growth changes sharply at this point. The first inter-

node did not elongate as much on the second day as it did on the first, hence the curve for this day is everywhere below the first one. Very interesting curves can be produced when several plants are compared, or when the increments of the various internodes of the same plant are recorded simultaneously.

The writer is now working in cooperation with the L. E. Knott Apparatus Company on a new model, which involves a different mechanism for opening the circuit. This machine will be smaller, and it is hoped that it can be put on the market at a very low cost.

HARVARD UNIVERSITY
LABORATORY OF PLANT PHYSIOLOGY

BRIEFER ARTICLES

SOME PLANTS OF WESTERN AMERICA

Several collections of plants from western America have recently been submitted to the writer for identification, and among them a number have been found of especial interest, either because of their geographical distribution or because they represent species which apparently have not been described hitherto; these may be recorded and diagnosed as follows:

ROMANZOFFIA UNALASCHCENSIS Cham. in Nees. Hor. Phys. Berol. 72, *t.* 14, 1820.—Specimens collected on the northeast aspect of vertical cliffs, three feet above high sea-level, Albert Head, British Columbia, 6 June, 1907, *Dr. C. F. Newcombe*, no. 324 (hb. Field Museum, cat. no. 250181) correspond in all essential details with a part of the original material in the Gray Herbarium on which the above species was founded. This station extends the range of the species considerably south from previously recorded localities.

Castilleja arachnoidea, n. sp.—Herbacea perennis; caulibus caespitosis erectis 2–3 dm. altis in partibus inferioribus crispo-hirsutis, superioribus arachnoideo-tomentosis; foliis 1.5–4 cm. longis linearibus vel anguste lanceolatis et integris plerumque trifido, laciniis linearibus acutis patentibus, lobo intermedio majore et saepe trifidis; inflorescentiis terminalibus dense spicatis 10–13 cm. longis; bracteis plerumque trifidis, lobo intermedio integro et obtuso vel apice trilobulato; calyce 15–17 mm. longo extrinsecus piloso antice et postice subaequaliter fisso; lobis lateralibus profunde partitis, laciniis lineare-lanceolatis acutis 7–10 mm. longis; corolla 17–20 mm. longa extrinsecus pubescente flava vel lobis in sicco paululo rubellis; galea erecta circiter quadruplo brevior quam tubus; labium trilobum 5–6 mm. longum; capsula oblonga 10–12 mm. longa acuminata acuta glabra.

On mountain summits near Marble Mountain, Siskiyou County, Cal., altitude 2000 m., 6 August, 1908, *Geo. D. Butler*, no. 422 (hb. Field Museum, cat. no. 276765).

In general habit this species resembles *C. Lemmoni* Gray, *C. pilosa* (Gray) Rydb., *C. pratensis* Heller, and *C. oresbia* Greenm.; it also approaches *C. ambigua* Jones, but differs in having a shorter corolla and in the nature of the pubescence. The arachnoid tomentum, long dense spikes, and conspicuous long lower lip of the corolla are the striking characters of the species.

Castilleja schizotricha, n. sp.—Herbacea perennis tota planta substellato-albido-tomentosa; caulibus caespitosis simplicibus erectis vel ascendentibus 1–1.5 dm. altis; foliis lineari-lanceolatis et integris vel trifidis 1–1.5 cm. longis 2–5 mm. latis, laciniis linearibus acutis patentibus; inflorescentiis purpureis terminalibus dense spicatis 5–9 cm. longis; bracteis saepissime trifidis circiter 1.5 cm. longis, lobis lateralibus linearibus acutiusculis, lobo intermedio lanceolato-oblongo acuto; calyce 15–17 mm. longo extrinsecus substellato-albido-tomentoso et stipitato-glanduloso antice et postice aequaliter fisso, laciniis lateralibus profunde partitis lineari-attenuatis acutis dense substellato-tomentosis; corolla purpurea 15–17 mm. longa, galea erecta 4 mm. longa circiter quater brevior quam tubus, labio circiter 4 mm. longo basi triplicato, labii lobis lineari-oblongis 2 mm. longis obtusis; capsula oblonga 8–10 mm. longa brevi-acuminata acuta glabra.

On summit of mountain, near Wooly Creek, Siskiyou County, Cal., altitude 1830 m., 5 August, 1908, *Geo. D. Butler*, no. 423 (hb. Field Museum, cat. no. 276766).

The species here described is apparently most nearly related to *C. brachyantha* Rydb., *C. Covilleana* Hend., and *C. pilifera* Nels. From all these it is readily separated by the branched hairs and the characters of the calyx.

Senecio Suksdorfii, nom. nov.—*S. Adamsi* Howell, Fl. N.W. America **1**:379, 1903, not *S. Adamsii* Cheesm. Trans. N.Z. Inst. **28**:536, 1896. Mr. HOWELL'S specific name for this plant coincides so closely with the name given by Mr. CHEESEMAN to a New Zealand species of this genus that it seems desirable to give our American plant a new specific name; and the writer takes pleasure in associating therewith the name of Mr. W. N. SUKSDORF, who has done so much to further our knowledge of the plants of Washington.

Hereto are referred the following: on rocky ridges, Mt. Paddo (Adams), Washington, altitude about 2155 m., 9 August, 1882, *W. N. Suksdorf* (hb. Gray, hb. Geol. Surv. Canada, and hb. Field Museum); east of Mt. Adams, August, 1892, *L. F. Henderson*, no. 2309 (hb. Gray); Yakima region, 1883, *T. S. Brandegee*, no. 915 (hb. Gray); Indian Henry Park, September, 1909, *J. B. Tarleton*, no 62 (hb. Field Museum); at the base of granite cliffs, source of the Imnaha, Wallowa Mts., Oregon, altitude 2690 m., 14 August, 1906, *Wm. C. Cusick*, no. 3131 (hb. Field Museum); on Mt. Rose, Nevada, altitude 2970 m., 29 July, 1909, *A. A. Heller*, no. 9896 (hb. Field Museum).

Senecio (§ AMPLECTENTES) **Websteri,** n. sp.—Herbaceus perennis; caulibus erectis vel ascendentibus 1.5–2 dm. altis parce floccoso-tomentulosis; foliis inferioribus petiolatis subovatis vel oblongo-obovatis 8–12 cm. longis 1.5–4.5 cm. latis acutis denticulatis vel sinuato-dentatis

basi decurrentibus membranaceis utrinque arachnoideo-tomentulosis plus minusve glabratis, petiolis alatis, foliis superioribus sessilibus lanceolatis irregulariter dentatis; pedunculis elongatis usque ad 8 cm. longis unicapitatis; capitulis 1.8–2 cm. altis multifloris radiatis subnutantibus; involucris campanulatis calyculatis; squamis involucri lineari-lanceolatis 13–15 mm. longis apice acutis penicillatis extrinsecus arachnoideo-tomentulosis; floribus femineis 12–15, ligulis lanceolato-oblongis 12–15 mm. longis 3–4 mm. latis flavis; floribus disci numerosis, corollis ca. 8.5 mm. longis; pappi setis albidis subaequantibus; achaeniis glabris.

On talus slopes of Mt. Angeles, Clallam County, Washington, altitude about 2000 m., 2 September, 1909, *E. B. Webster*, no. 109 (hb. Field Museum cat. no. 251971).

In habit *S. Websteri* is similar to *S. seridophyllus* Greene which, however, is glabrous throughout and has smaller heads and shorter rays. In foliar characters *S. Websteri* resembles *S. Elmeri* Piper, but differs in having much larger and solitary heads. Mr. E. B. WEBSTER of Port Angeles, by whom the specimens were collected, in commenting on the plant, states: "There are possibly a hundred plants in all, a few growing at the northern side of the base of one of the pinnacles, the remainder being scattered along the narrow rocky talus for possibly 1000 ft.; on the slope at the base of the pinnacle *Arnica cordifolia* Hook. and *Heuchera racemosa* Wats., both rare on Mt. Angeles, were associated with the *Senecio*, and somewhat lower down *Hedysarum occidentale* Greene and *Arabis Lyallii* Wats. were growing along with it."—J. M. GREENMAN, *Chicago*.

SOIL MOISTURE IN THE COTTONWOOD DUNE ASSOCIATION OF LAKE MICHIGAN

(WITH ONE FIGURE)

The following data regarding the range of soil moisture in the cottonwood dune association upon the shores of Lake Michigan seem to be of sufficient interest to warrant their publication in advance of the results of more extensive studies of the same sort now in progress. The work of COWLES[1] upon its general ecological relations and that of the writer[2] upon the evaporating power of the air have shown this to be an open association of a single tree species, together with a scanty undergrowth

[1] COWLES, H. C., The ecological relations of the vegetation of the sand dunes of Lake Michigan. BOT. GAZ. **27**:95–391. 1899.

[2] FULLER, G. D., Evaporation and plant succession. BOT. GAZ. **52**:193–208. 1911.

of shrubs and grasses, developing upon more or less rapidly moving dunes, possessing a very high rate of evaporation, exhibiting many strongly xerophytic characters, and almost entirely dependent upon vegetative reproduction for its maintenance. The almost complete absence of herbaceous undergrowth and the expanse of bare sand give it a desert-like aspect, but below the superficial layer of dry sand an abundant and unfailing water supply has been found.

From the beginning of May to the end of October 1911 duplicate samples of about 125 grams of soil were taken weekly at depths of 7.5 cm. and 25 cm., the soil dried at 104° C., and the ratio of water to the dry weight of soil found to range from 2 to 8 per cent, an apparently very inadequate amount.

Until recently no satisfactory means of relating such soil moisture determinations to plant growth have been available but the "wilting coefficient" of BRIGGS and SHANTZ[3] now indicates the limit of soil water content above which growth must occur, although plants will live and continue to draw water from the soil much below this limit. Further, the same workers have shown that many plants differ very little in their wilting coefficients from the standard Kubanka wheat. As under ordinary conditions a water supply very little above that at which wilting occurs is sufficient for some growth, the difference between the soil moisture actually present at any time and the wilting coefficient of the soil represents approximately the amount of water available for purposes of growth, and this, in the absence of a better term, may be referred to as "growth water."

Following the methods of BRIGGS and SHANTZ (*loc. cit*), the wilting coefficient of the dune soil was found to be 0.75 per cent at both depths, the absence of humus accounting for this similarity. Graphically representing this wilting coefficient and plotting the soil moisture determinations as graphs having the weekly intervals as abscissae and the percentage of water present in the soil as ordinates (fig. 1), it will be seen that the moisture present in the soil of the cottonwood dune is at all times more than double the wilting coefficient, or in other words there is always present at least twice the amount of water necessary for the growth of such a plant as wheat. Throughout the most arid portion of the season, namely the ten weeks beginning with the first of July, the surplus or growth water averages 2.2 per cent, showing that,

[3] BRIGGS, L. J., and SHANTZ, H. L., The wilting coefficient for different plants and its indirect determination. U.S. Dept. Agric., Bur. Pl. Ind. Bull. 230, 1912; also BOT. GAZ. **53**:20–37, 229–235. 1912.

considered upon the basis of its soil moisture, the association is decidedly mesophytic. The causes of the xerophytic character of the vegetation must be sought in the high evaporating power of the air and in the instability of the substratum. These factors, however, doubtless react upon the surface of the soil and tend to conserve the soil water by constantly maintaining a dry surface mulch. The constant presence of a sufficient amount of moisture perhaps will help to explain the readiness

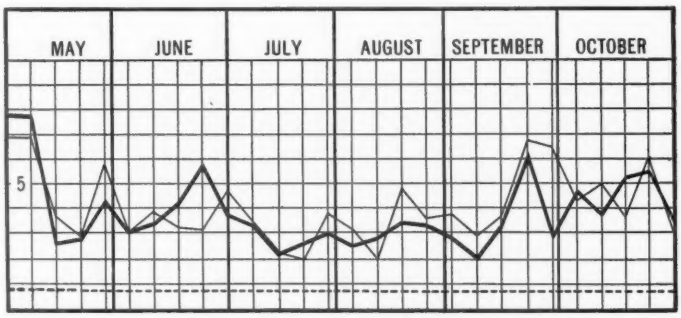

FIG. 1.—Graphs showing the range of soil moisture in the cottonwood dune; the heavy line at 7.5 cm. and the light line at 25 cm. depth; wilting coefficient represented by a broken line.

with which vegetative reproduction occurs within the association, while the shifting sand and high rate of evaporation may account for the almost entire absence of seedlings of any sort.

From these scanty data it would seem that determinations of soil moisture, related to plant growth through the wilting coefficients of the soil, will afford an efficient means of making quantitative studies of the water supplies of the subterranean parts of plant associations, and, as in the present instance, enable students of ecology to analyze more closely the effects of the various factors influencing the production of any particular plant association.—GEO. D. FULLER, *The University of Chicago.*

CURRENT LITERATURE

BOOK REVIEWS

Texts for secondary schools

The authors of *Applied biology*[1] do not wish to indicate by the title any unusual predominance of economic material. Their book is a text of general biology, in which the materials used do not differ particularly from those commonly found in secondary texts of botany and zoology. This book is certainly very much superior to that type of textbook in general biology which consists of three wholly distinct books bound within the same cover, but one may find reason for doubting that even here we have a satisfactory organization of botany, zoology, and human physiology into a single instructional unit. It is of interest to note that but 10 per cent of the book is sufficiently "general" to hinder its transfer bodily to textbooks of botany, zoology, or physiology. There are a number of minor botanical errors, but these will not hinder the book from being successfully used where it is desired to conduct a general biology course. It is unfortunate that many of the cuts were copied from other books with the original labeling, and this is in many cases not explained by the legend.

The textbook of botany by ANDREWS[2] is evidently a revision of the earlier book by the same author, intended to meet the present demand for instruction in botany "with especial reference to agriculture, economics, and sanitation." It quite fails to measure up to the demand. The insertion of a few paragraphs on economic subjects is not sufficient to metamorphose a book into the type for which the present popular demand calls. Judged by any standards other than the present popular enthusiasm for applied material, the text of the book would be considered satisfactory. The illustrations are much less satisfactory. A large number of the cuts have been copied, sometimes without credit. The photographs have been retouched and otherwise modified to the point of falsification. It seems unpardonable in these days of easy illustration to attempt to show the characteristics of climbers by a "faked" photograph of a grape vine, or to illustrate important principles of plant breeding by a drawing with the same scientific and artistic merit as a country newspaper cartoon. One cannot but feel that in its present form the book is not worthy of its author or of its publishers.

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[1] BIGELOW, M. A., and BIGELOW, A. N., Applied biology. 8vo. pp. xi+583. *figs. 166.* New York: Macmillan. 1911.

[2] ANDREWS, E. F., A practical course in botany, with editorial revision by F. E. LLOYD. 8vo. pp. ix+374. *figs. 511.* New York, Cincinnati, Chicago: American Book Co. 1911.

The book by PEABODY and HUNT[3] is principally interesting as illustrating a very distinct recent tendency in elementary botanical instruction. It will be recalled that not long since our elementary texts emphasized morphology and anatomy. Of late the new books have been giving more and more space to the physiology and ecology of seed plants. The book under review carries this to the extreme by relegating the morphology to a final "optional" chapter. Such an extreme position will scarcely be accepted generally, but the tendency in that direction is unmistakable.

The tendency toward the abbreviation of the morphological part of the work is evident also in *Experimental botany*.[4] The last chapter in the book takes up the "cryptogams." This book is a laboratory manual rather than a textbook, though there is a small amount of descriptive text. Its unique feature is in the experimental attitude which is maintained throughout. The author feels that botany should be taught experimentally in the same sense that physics or chemistry is so taught; the selection of physiological materials follows naturally. The laboratory directions appear to be workable. A large number of the experiments are new to elementary texts. The new point of view and the new experiments make it a stimulating book for teachers.

The laboratory manual by FRYE and RIGG[5] is intended to meet the needs of teachers on the Pacific slope. The species suggested for laboratory work are selected with reference to the western flora. The directions for work are well written, and it is in every way an excellent little book. While it is written with western conditions in mind, and must be particularly welcome in that part of the country, it would be quite usable in the East as well.—W. L. EIKENBERRY.

MINOR NOTICES

Flora of Porto Rico.—The publication of the fourth fascicle of Vol. IV of URBAN'S *Symbolae Antillanae*,[6] which includes the sympetalous groups from the genus *Tamonea* of the Verbenaceae to the end of the Compositae, under the subsidiary title of *Flora portoricensis*, brings to a close a consideration of one of the most interesting of our insular floras. New species are described in *Priva*, *Dicliptera*, and *Psychotria*. The taxonomic part is followed by a *Nachwort*, in which the author sets forth the purpose of the work and reviews

[3] PEABODY, J. E., and HUNT, A. E., Elementary plant biology. 8vo. pp. xvi+207. *figs. 91*. New York: Macmillan. 1912.

[4] PAYNE, F. O., Manual of experimental botany. 8vo. pp. 272. *figs. 117*. New York, Cincinnati, Chicago: American Book Co. 1912.

[5] FRYE, T. C., and RIGG, G. B., Laboratory exercises in elementary botany. 8vo. pp. xxii+139. Boston: Ginn & Co. 1911.

[6] URBAN, IGNATIUS, Symbolae Antillanae seu fundamenta florae Indiae Occidentalis, Vol. IV, fasc. 4. pp. 529–771. Flora portoricensis. Leipzig: Fratres Borntraeger. 1911.

briefly the circumstances under which the study was begun, developed, and brought to completion. A brief but interesting chapter is devoted to a history of botanical exploration in Porto Rico from the earliest collections made in 1785–1786 to the recent expeditions by different members of the staff of the New York Botanical Garden. A careful tabulation shows that 2056 species, representing 167 families of Pteridophytes and Phanerogams, are known from the island at the present time. Of this number 271 species, or 13.13 per cent, are peculiar to the island. The families best represented in numbers of species are: Polypodiaceae (182), Leguminosae (136), Gramineae (122), Compositae (90), Orchidaceae (86), and Cyperaceae (85). From a detailed analysis of the species recorded, Professor URBAN concludes that the flora of Porto Rico is most closely allied to that of South America. A very complete index to the Latin and vernacular names terminates the volume. The work forms a reliable and authoritative basis for future investigations on the flora of this interesting and economically important insular territory.—J. M. GREENMAN.

Flora of Formosa.—Since the publication of the *Enumeratio plantarum Formosanarum* in 1906 and the *Flora montana Formosae* in 1908, investigations on the flora of the island of Formosa have been pushed forward with astonishing vigor, which is amply attested to by the appearance of another volume entitled *Materials for a flora of Formosa*.[7] The author in the present volume has attempted to enumerate all species recorded from the island since the publication of the works mentioned above. Flowering plants, ferns, and fern-allies only are included, and these are chiefly from the mountainous regions of the island. Over 700 species are listed, representing 343 genera and 109 families, thus making the total number of species known up to the present time 2660, representing 836 genera and 156 families. The work of identification of the plants on which this contribution to knowledge is based has been carried on at Tokyo, Kew, Paris, Berlin, and St. Petersburg, and over 300 species and several varieties are characterized as new to science. The location of the island of Formosa is such that its flora is composed of elements common to Japan, China, India, and the Malayan region. The large number of novelties recorded is suggestive of a very rich and varied flora, and indicates, moreover, that Formosa is still a fruitful field for further taxonomic investigation.—J. M. GREENMAN.

NOTES FOR STUDENTS

Biology of rusts.—MÜHLETHALER, who has made a large number of cultural experiments with the crown rusts of grasses in Switzerland, has given a complete account of his investigations, a part of the results of which have already been published in a preliminary account.[8] Since DEBARY'S demon-

[7] HAYATA, B., Materials for a flora of Formosa. Jour. Sci. Coll. Tokyo **30**:1–471. 1911.

[8] Rev. BOT. GAZ. **51**:157. 1911.

stration of the connection between the crown rusts of grasses and the aecidia occurring on species of *Rhamnus*, these rusts have been more especially investigated by ERIKSSON and by KLEBAHN, with the result that two species have been differentiated: *Puccinia coronata* (Corda) Kleb. with aecidia chiefly on *Rhamnus Frangula;* and *P. coronifera* Kleb. with aecidia chiefly on *R. cathartica*. These comprise several form-species whose teleutospore generation in each case is confined to a small group of grasses. To these collective species MÜHLETHALER[9] has added a third, described as *P. alpinae-coronata* with aecidia on *Rhamnus alpina* and *R. pumila*.

The cultural work, which covers an unusually large number of infection experiments, emphasizes more strongly the facts already suggested in the work of KLEBAHN and of ERIKSSON, that the crown rusts are not so strictly limited, in their specialization, to certain hosts as some of the earlier experiments would seem to indicate, and that some of the form-species formerly established should not be kept separate. Thus, for example, the form occurring on the members of the genus *Lolium* can be transferred to members of the genus *Festuca*, showing that a sharp separation of f.sp. *Lolii* and f.sp. *Festucae* is impossible. There is also evidence to show that the degree of specialization of different forms is not the same in different regions, a fact which JACZEWSKI[10] has already pointed out in his studies on Russian grain rusts. Unfortunately, the present experiments were not continued long enough to bring out all the interrelationships of the different form-species. The cultures reported comprised (1) infection of grasses either directly by aecidiospores, or indirectly by uredospores derived from the aecidiospore infection; and (2) infection of members of the genus *Rhamnus* by teleutospores from these grasses. The aecidial material was mostly gathered in its native habitat, so that there could be no assurance of its purity, and the experiments were not continued long enough to isolate with certainty the different form-species whose aecidia occur on the same species of *Rhamnus*. For these reasons, no attempt is made in this review to distinguish between the different form-species. For experimental evidence bearing on this point the original paper must be consulted.

Aecidiospores from *Rhamnus Frangula*, or the uredospores derived from these, infected *Phalaris arundinacea*, *Calamagrostis arundinacea*, *Glyceria fluitans*, and *Anthoxanthum ordoratum* (doubtful). Teleutospores (sporidia) from *Phalaris arundinacea* infected *Rhamnus Frangula*, *R. Purshiana*, *R. californica*, *E. imeretina* (spermagonia), and *R. alaternus* (spermagonia).

Aecidiospores from *Rhamnus cathartica*, or the resulting uredospores, infected, in one series, *Lolium perenne*, *L. rigidum*, *L. italcum*, *L. temulentum*, *L. remotum* var. *aristatum*, *Festuca elatior*, *F. arundinacea*, *Phleum pratense* (poorly), and *Dactylis glomerata* (poorly). The teleutospores from *Lolium*

[9] MÜHLETHALER, F., Infektionsversuche mit *Rhamnus* befallenden Kronenrosten. Centralbl. Bakt. II. **30**:386–419. 1911.

[10] Rev. BOT. GAZ. **51**:75. 1911.

perenne and *L. rigidum* infected *Rhamnus cathartica, R. utilis, R. dahurica, R. saxatilis,* and *R. imeretina.* In another series the aecidiospores from *R. cathartica,* or the resulting uredospores, infected *Bromus erectus* and its var. *condensatus, B. sterilis, B. inermis, B. tectorum, B. secalinus, B. commutatus, Festuca varia, F. arundinacea, F. alpina, F. gigantea, F. violacea, F. rubra* (poorly), and *Lolium perenne* (1 sorus). The teleutospores from *Bromus erectus* (collected in nature) infected *Rhamnus cathartica, R. utilis, R. saxatilis,* and *R. dahurica;* and the teleutospores from the foregoing aecidial infection on *Festuca arundinacea* infected *R. cathartica, R. utilis, R. dahurica, R. saxatilis, R. imeretina,* and *R. alaternus.*

Aecidiospores from *Rhamnus pumila* infected *Calamagrostis varia,* and the teleutospores from this grass infected *R. pumila, R. alpina, R. Purshiana, R. californica, R. imeretina,* and *R. Billardi* (spermagonia).

The following cultural experiments with rusts are reported by MAYOR[11] in Neufchatel, Switzerland. The form of *Puccinia* on *Carex digitata* infected *Ribes alpinum* and *R. Grossularia,* and that on *C. glauca* infected *R. alpinum,* the reverse sowing being also made in the latter case. The forms of *Puccinia* on these two species of *Carex,* therefore, belong to the Ribesii-Caricis group of KLEBAHN, but the data are insufficient for determining if they belong to any of the five species into which KLEBAHN has divided that group. To the hosts of *Puccinia longissima* whose alternate generations occur on species of *Koeleria* and *Sedum* the author adds *K. valesiaca,* teleutospores from that host having infected *Sedum reflexum.* A form of *Puccinia* from *Carex muricata* infected *Crepis biennis* but not *Taraxacum.* It seems, therefore, that this rust is distinct from *P. sylvatica. Puccinia Actaeae-Elymi* is described as a new form with teleutospores on *Elymus europaeus* and aecidia on *Actaea spicata.* This form does not infect *Triticum caninum* and therefore is distinct from *P. Actaeae-Agropyri* Fischer, which has teleutospores on that host and aecidia on *Actaea spicata.*

A series of infection experiments made by DIETEL[12] with *Hyalospora Polypodii* on *Cystopteris fragilis* is the first attempt at cultural experiments with a fern rust. *Hyalospora* produces thin-walled and thick-walled uredospores, and apparently only rarely teleutospores. Sowings were made on *Cystopteris* both with fresh uredospores and with uredospores that had been left in the open during the winter. In both cases infection occurred easily. In the newly formed sori thin-walled uredospores were first produced, and these were followed later by the thick-walled form. Teleutospores were not observed. The author believes, as a result of these experiments and the rare occurrence of the

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[11] MAYOR, EUG., Récherches expérimentales sur quelques Urédinées hétéroiques. Ann. Mycol. **9**:341–362. *figs.* 3. 1911.

[12] DIETEL, P., Über einige Kulturversuche mit *Hyalospora Polypodii* (Pers.). Magn. Ann. Mycol. **9**:530–533. 1911.

teleutospores, that this rust normally maintains itself by means of the hibernating uredospores.

In a paper which is the eleventh of a series of reports on his well-known cultural work with plant rusts, carried on since 1899, ARTHUR gives the results of the cultures of 1910.[13] The work of that year was under the immediate charge of Miss IRMA A. UHDE. Sowings of spores of 21 species of rusts on a large number of possible aecidial hosts gave no infections. Successful cultures with 34 species supplemented or confirmed the results previously obtained either by the author or by other American and European investigators. The following six forms have been connected with their antithetic generation for the first time: *Puccinia Crandalii* Pam. & Hume on *Festuca confinis* Vasey and *Symphoricarpus racemosus* Michx.; *P. quadriporula* Arth. on *Carex Goodenovii* J. Gay and *Aster paniculatus* Lam.; *Puccinia Lithospermi* E. & K. on *Evolvulus pilosus* Nutt., autoecious; *Uromyces acuminatus* Arth. on *Spartina Michauxiana* A. S. Hitch. and *Polemonium reptans* L.; *Coleosporium Vernoniae* B. & C. on *Vernonia crinita* Raf. and *Pinus Taeda* L. (aecidiospores sown on *Vernonia*); and *Melampsora Albertensis* Arth. on *Populus tremuloides* Michx. and *Pseudotsuga mucronata* (Raf.) Sudw.

The host relations of some of the *Peridermium* rusts in Nova Scotia have been studied by FRASER,[14] who, in addition to a number of field observations, reports cultures with the following forms. Teleutospores of *Melampsoropsis Cassandrae* (Peck and Clinton) Arth. from *Chamaedaphne calyculata* (L.) Moench sown on *Picea rubra* (Du Roi) Dietr. produced *Peridermium consimile* Arth. & Kern. Teleutospores of *M. abietina* (Alb. & Schw.) Arth. from *Sedum groenlandicum* Oeder also sown on *Picea rubra* produced *Peridermium abietinum* (Alb. & Schw.) Thüm. *M. ledicola* (Peck) Arth. from *Ledum* produced *Peridermium decolorans* Peck on *Picea canadensis*. One form, *Uromyces Peckiananus* Farlow on *Distichlis spicata* (L.) Greene, not belonging to the *Peridermium* rusts, produced aecidia on *Atriplex patula* var. *hastata* (L.) Gray and *Chenopodium album* L.

FISCHER'S[15] review of the work done on the biology of rusts in 1910 will be of interest to students of this group.—H. HASSELBRING.

Cytology of the Basidiomycetes.—Among the many papers which have lately appeared on the cytology of the higher fungi, three are of more than usual interest. FRIES,[16] in a brief paper on *Nidularia*, finds the mycelium and young basidia binucleated, the nuclei having the chromatin in two conspicuous masses. The nuclei increase in size with the growth of the basidium, gradually

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[13] ARTHUR, J. C., Cultures of Uredineae in 1910. Mycologia **4**:7–33. 1912.

[14] FRASER, W. P., Cultures of some heteroecious rusts. Mycologia **3**:67–74. 1911.

[15] FISCHER, ED., Die Publicationen über die Biologie der Uredineen in Jahre 1910. Zeitschr. Bot. **3**:620–623. 1911.

[16] FRIES, ROB. E., Über die cytologischen Verhältnisse bei der Sporenbildung von *Nidularia*. Zeitschr. Bot. **3**:145. 1911.

approach, and fuse as they near the apex. The fusion nucleus increases greatly in size and forces the vacuoles, which had hitherto occupied a position between the nucleus and the end of the basidium, toward the periphery. Stages in this process are hard to follow because of the rapidity of development, but finally the single nucleole comes to lie in a tangle of chromatin in an otherwise clear nucleus. This seeming synapsis leads to a spireme stage which must be of rather long duration because of the many found. Parallel fibers are noted which become more conspicuous as the fibers shorten and segment, giving a characteristic diakinesis. At this stage the nuclear membrane has disappeared, but there is as yet no trace of spindle fibers. In the lower portion of the basidium there appears at this time a network of fibers, which finally partly surround the nuclear material, but which, however, seem to have nothing to do with the formation of the spindle. The long narrow spindle, seemingly of only three fibers, suddenly makes its appearance. Conspicuous centers are noted, but there is no trace of any radiations from either center. No definite equatorial plate was formed, but during anaphase 6–8 chromosomes were noted, one-half of which passed to either pole. No resting stage follows the division, the secondary spindles appearing at once, shorter, broader, and having two chromosomes at each pole when the process is completed. Four rather large nuclei are formed and gradually migrate toward the base of the basidium. Sterigmata develop and the nuclei become beak-shaped and pass into the developing spore and again divide. In some instances it was found that the nuclei begin to divide while still in the basidium, the process being completed when the spore is reached.

KNIEP[17] finds in the mycelium from a single spore only one nucleus in each cell, and this condition persists even in cultures a year old. He finds in young cultures (3–4 weeks) that basidia are produced without the formation of a normal fruit body. These basidia may or may not be developed from terminal cells, and each contains a single nucleus. This is somewhat larger than the nuclei of the mycelium, but according to KNIEP is never due to a fusion. Each contains a conspicuous nucleole and a dense tangle of chromatic material connected to the nuclear membrane by numerous strands. The nucleus increases in size with the growth of the basidium, the nuclear material becomes granulated, at times parallel threadlike portions are noted, the nucleole decreases in size, and the dark-staining chromatic material becomes very much contracted. At this stage conspicuous double threads are observed. This stage, which very much resembles synapsis, precedes the formation of a spireme, during which the nucleus migrates to the apex of the basidium, where follows a rapid contraction of chromatic material accompanied by the disappearance of the nuclear membrane. KNIEP was able to count at this stage four masses of chromatin from which radiations extended into the cytoplasm, giving very

[17] KNIEP, HANS, Ueber das Auftreten von Basidien im einkernigen Mycel von *Armillaria mellea* Fl. Dan. Zeitschr. Bot. **3**:381. 1911.

much the appearance of a multipolar spindle. These fibers bear no relation to the true spindle which now makes its appearance. No centrosomes were observed, and only four chromosomes of which two passed to either pole. The chromosomes changed greatly in shape as they moved along the spindle, indicating a very plastic nature. The second division follows at once, giving rise to the nuclei which pass into the spores. In some instances a third division takes place within the basidium, and as a result there is a degeneration of four of the nuclei.

FRIES[18] finds in *Hygrophorus conicus* that the cells of the trama contain one or more pair of nuclei, while the cells of the subhymenium have only a single nucleus, each having a conspicuous nucleole and two distinct masses of chromatin. Basidia, even the youngest, are uninucleated with the same double nature of the chromatic content. Growth of the basidium is accompanied by a corresponding growth in size of the nucleus, and the chromatin assumes the nature of a long delicate spireme thread. Following closely upon this there is a disappearance of the nuclear membrane and a sudden contraction of the spireme into a compact mass surrounded by a granular (plasma) cytoplasm. Spindle fibers now appear (no centrosome was found) and two chromosomes are seen to pass to each pole. The daughter nuclei, which at this stage lie near the apex of the basidium, are fully reconstructed and move toward the base of the basidium, where they remain while the sterigmata are developed. As soon as the sterigmata are fully formed, the nuclei in most cases become beaked and pass into the spore and divide; in other instances the division is partly completed in the basidium.

The first of these papers describes a process which is usually considered the typical method of nuclear behavior in the higher Basidiomycetes. We have here the fusion of nuclei, a synapsis, a spireme (double in its nature), a heterotypic followed by homotypic division.

In the second paper we have no fusion of nuclei, but stages are described and figures given which compare favorably with those of the preceding paper, although the author does not admit of chromosome reduction.

The third paper describes a form unique in that the cells of the trama contain more than one nucleus, while the basidium contains but one, and this according to the author is not a fusion nucleus. Therefore the division in the basidium is not a reduction division.—E. M. GILBERT.

Amanita.—Dr. RENÉ FERRY, former editor of the *Revue Mycologique*, has recently published a paper of a monographic nature dealing with the "deadly" Amanitas,[19] with special reference to their botanical characters,

[18] FRIES, ROB. E., Zur Kenntnis der Cytologie von *Hygrophorus conicus*. Svensk. Botanisk. Tidskrift **5**: 242–251. 1911.

[19] FERRY, RENÉ, Étude sur les Amanites; les Amanites mortelles. *Amanita phalloides, Amanita verna,* et *Amanita virosa*. Rev. Mycologique. Suppl. 1. pp. 1–96. *pls. 1–8*. 1911. Saint-Dié (Vosges), France. 4.50 fr. On sale by the author.

chemistry, and toxicology. The first part is devoted to descriptions of the three species which the author believes are responsible for the deaths from mushroom poisoning: *Amanita phalloides*, *A. verna*, and *A. virosa*. *A. phalloides* is recognized as a very variable species. Good descriptions are given of these species and of the varieties of *A. phalloides*, and the determination of the species is further aided by colored illustrations, including the American varieties which are copied from PECK's Report. Not all students may agree with FERRY in his treatment of these species, but it is doubtful if anyone can at present, or even in the near future, limit and characterize the species of *Amanita* in a manner which will be acceptable to all. The author's object, however, is not so much to limit precisely the natural species as it is to present characters and illustrations by which the deadly species of this genus may be recognized by those who have little technical knowledge of the fungi.

The second part, covering more than 70 pages, is a thorough discussion of the recent work, in Europe and America, on the chemistry and toxicology of these three species, particularly of *A. phalloides*. There are two important toxic principles. Phalline (KOBERT) or "Amanita-hemolysine" (FORD) is a hemolytic agent which dissolves the red blood corpuscles. Its chemical nature is uncertain (FORD), but temperatures of 65–70° C. destroy it, so that thorough cooking renders this poison innocuous. The other toxic principle is "Amanita-toxine" (FORD), which is not destroyed by heat, and for which no antidote is known. Its chemical nature is unknown. Hemolysine is found in certain of the edible fungi, for example *Amanita rubescens*, and this emphasizes the necessity of thorough cooking of all mushrooms. There is a thorough discussion of the symptoms of poisoning by these toxins, treatment, precautionary measures, experiments on immunization, etc. The work is a valuable one for those interested in the determination of these poisonous species, and particularly for the physician, pharmacist, etc.—G. F. ATKINSON.

Jurassic cones.—NATHORST[20] has described two new species of the Jurassic cone-impression known as *Cycadocarpidium*, has established definitely its identity with the leaf-genus *Podozamites*, and has discussed the relationship of this interesting gymnosperm. The leaves (*Podozamites*) are linear or elliptical, and seem, in certain species at least, to be borne on definite short shoots. The sporophylls (*Cycadocarpidium*) are much like the vegetative leaves, and are arranged in loose cones. Each sporophyll bears at its base two ovules, with pointed, winglike appendages. *Cycadocarpidium*, at first believed to be the fructification of a cycad related to the Zamieae, is considered by the author as a possible connecting form between cycadophytes and conifers. A fuller knowledge of both the vegetative and reproductive structures of the plant, however, lends little support to the theory of its cycadean affinity, and it seems

[20] NATHORST, A. G., Über die Gattung *Cycadocarpidium* (Nathorst) nebst einigen Bemerkungen über *Podozamites*. Kungl. Svensk. Vetensk. Handl. **46**: no. 8. pp. 11.

best included among those strange mesozoic conifers of whose structure and relationships so much is yet to be learned.—E. W. SINNOTT.

The carpophore of Agaricaceae.—An investigation of the development of the carpophore of several species of the Agaricaceae by BEER[21] brings still further evidence supporting the now generally accepted view that the hymeniun of the Agaricaceae arises endogenously, and not exogenously in the manner first described by HARTIG. As to the relative priority of the differentiation of the pileus and the hymenial primordium, BEER finds that in *Hypholoma fasciculari*s and *Clitocybe laccata* the pileus is differentiated first, while in *Armillaria mellea* the hymenium is the first structure to become visible. In this respect *Armillaria mellea* agrees with *A. mucida* as described by FISCHER, and with *Agaricus campestris* as described by ATKINSON. These forms show that the generalization of FAYOD, that the pileus is first differentiated in all cases, does not hold for all forms.—H. HASSELBRING.

A paper atmometer.—In an effort to obtain an instrument for the measurement of evaporation with temperature relations comparable to those of the foliage leaf, LIVINGSTON[22] has devised a paper cup atmometer, which is a modification of the Piche instrument. The advantages claimed for the new device are that as it contains a much smaller volume of water than the porous cup atmometer, it responds more promptly to changes in the external temperature. The surface of the paper cup may also be colored and the atmometer used for the measurement of light effects. This form of atmometer is likely to prove most useful in exact laboratory and controlled experiments, but will not replace the more durable clay cup for ecological field studies.—GEO. D. FULLER.

Composition of soil water and plant distribution.—The percentage of calcium and magnesium salts in solution in the soil water is believed by LANGERON[23] to give adequate explanation for many local peculiarities of plant distribution. To facilitate such studies he describes methods of water analysis which may be used in the field and laboratory, giving, with a minimum expenditure of time and effort, results sufficiently accurate to be related to differences in the composition of various plant associations. He has obtained promising results by applying his methods to the study of the bryophyte flora of the Bouche d'Erquy.—GEO. D. FULLER.

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[21] BEER, R., Notes on the development of the carpophore of some Agaricaceae. Ann. Botany **25**:683–689. *pl. 1.* 1911.

[22] LIVINGSTON, B. E., Paper atmometers for studies in evaporation. Plant World **14**: 281–289. 1911.

[23] LANGERON, MAURICE, Valeur de l'hydrotimétrie en géographie botanique pour l'étude des accidents locaux. Bull. Soc. Bot. France **58**: 236–245, 266–273, 327–336, 421–428. 1911.

GENERAL INDEX

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